AN ABSTRACT OF THE THESIS OF

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Title: The Effects of Biomechanical and Ecological Factors on Population and Community Structure of Wave-exposed, Intertidal Macroalgae

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I examined the biomechanical factors that influence the sizes of intertidal macroalgae by studying a population of *Fucus gardneri* at Fogarty Creek Point, OR. I constructed a mathematical model to predict optimal sizes and probabilities of survival for *Fucus* under conditions of high and low wave exposure. Predicted optimal sizes of *Fucus* closely matched the mean observed sizes of plants collected from wave-exposed and protected locations. To test this hypothesis in the field, I reciprocally transplanted *Fucus* between wave-exposed and wave-protected sites and found that the degree of wave exposure did not affect survival, but did influence size. Large *Fucus* were tattered by waves at exposed sites, and small *Fucus* grew at protected sites. These results support the hypothesis that wave forces can set mechanical limits to size in *Fucus*.

I experimentally examined the relative influences of wave-induced disturbance, competition and predation on the sea palm, *Postelsia palmaeformis* and its understory community at a wave-exposed site at

Depoe Bay, OR. *Postelsia* recruitment was affected by seasonal variations in disturbance and was greatest in areas disturbed in winter. *Postelsia* were most abundant at mid-zone, wave-exposed sites, and their restriction to wave-exposed sites seems to be due both to; 1) the occurrence of predictable winter disturbances at these sites which remove mussels, thereby stimulating sea palm growth from the underlying rock, and 2) high water motion which enhances sea palm growth by increasing nutrient exchange and photosynthesis and preventing desiccation at low tide.

Competition, disturbance and grazing were all important factors in structuring the *Postelsia* understory community. *Postelsia* were dominant competitors and their holdfasts overgrew low-lying plants which were torn loose with *Postelsia* when this kelp was dislodged by winter storm surf. In the absence of this predictable, seasonal disturbance, competitive understory species, such as *Corallina* dominated primary space. Intermediate levels of disturbance allowed for the highest understory species diversity. Limpets played a keystone role by grazing *Postelsia*, the competitive dominant during most of the year, and maintained high levels of species diversity in the algal understory.

The Effects of Biomechanical and Ecological Factors on Population and Community Structure of Wave-exposed, Intertidal Macroalgae

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

THE EFFECTS OF BIOMECHANICAL AND ECOLOGICAL FACTORS ON POPULATION AND COMMUNITY STRUCTURE OF WAVE-EXPOSED, INTERTIDAL MACROALGAE

Chapter I

GENERAL INTRODUCTION

Sousa (1984a) describes two features which characterize all natural communities. The first is that they are dynamic systems. The relative abundances of species, as well as the age and size-structures of the component populations all change over time (Connell and Slatyer 1977, Connell and Sousa 1983). The second feature is that they are spatially heterogeneous. Communities may be seen as mosaics of patches identified by spatial discontinuities in the distributions of populations (Watt 1947, Wiens 1976, Harper 1977, Paine and Levin 1981, Dayton et al. 1984, Dethier 1984, Sousa 1984b, Menge et al. 1993). Disturbance is a source of temporal and spatial heterogeneity in the structure and dynamics of natural communities (Sousa 1984a). Sousa (1984a) suggests that much of the spatial and temporal heterogeneity one observes in natural communities may be due to the differential expression of life history attributes under different disturbance regimes. However, heterogeneity in the environmental conditions induced by disturbance probably plays a key role in selecting among life history variants. A disturbance may be defined generally as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment" (Pickett and White 1985). In this

sense, both physical and biological processes may act as agents of disturbance (Harper 1977). The influence of disturbances on community or ecosystem structure is strongly dependent on the rate of resource release, its timing, spatial scale, magnitude and periodicity (Levin and Paine 1974, Connell 1978).

In the marine environment, wave action is a major agent of disturbance. The disruptive influence of moving water has been studied in marine habitats along temperate, rocky shores (Dayton 1971, Paine 1979, Sousa 1979, Paine and Levin 1981) and on tropical coral reefs (Connell 1978, Dollar 1982, Woodley et al. 1981). The regime of disturbance in marine habitats varies in space and time since wave action is maximal during seasons of high storm activity. Water motion along temperate rocky shores can produce some of the most powerful hydrodynamic forces on earth (Jones and Demetropoulos 1968, Denny 1987, 1988, 1991, Denny et al. 1985). Paradoxically, the surf zones of these wave beaten shores contain extremely diverse communities of plants and animals, many of which are sessile. The life cycles of many sessile organisms are strongly dependent on the occurrence of disturbance, since the persistence of many sessile populations depends on dispersal to sites suitable for recruitment. Many species depend on disturbance to create conditions favorable for the recruitment, growth and reproduction of their offspring.

The intertidal zones of wave-swept, rocky shores are ideally suited to ecological experimentation due to the high diversity of fast-growing species on a relatively small spatial scale, and over sharp gradients in physical conditions. Although much of our current understanding of community structure is based on experimental manipulations in this system (Paine

1966, 1974, Dayton 1971, Menge 1976, Lubchenco and Menge 1978), there is little mechanistic understanding of how wave-induced water motion affects ecology.

In this thesis, I examine how wave-induced water motion acts as an agent of disturbance on wave-swept shores, affecting the size, survival and community structure of marine macrophytes. In Chapter II, I examine how wave forces can influence the maximum sizes to which marine plants may grow. Based on recent experimental evidence that algae experience significant accelerational forces in oscillating flow (Gaylord et al. 1994), I constructed a mathematical model to predict probabilities of survival and optimal plant sizes under conditions of high and low wave exposure. I experimentally approached this question in the field using the common alga, *Fucus gardneri* which is found in both wave exposed and protected sites and occurs in a range of sizes from small to large, respectively along this wave exposure gradient. I reciprocally transplanted *Fucus* between the most wave exposed and protected areas at a rocky intertidal site in Oregon, and followed the survival and sizes of marked individuals over time. In Chapter III, I discuss how water motion and wave exposure influence the growth and survival of *Postelsia palmaeformis*, a common, annual intertidal kelp found in Oregon only at wave exposed locations. I also discuss how wave action, which peaks seasonally in winter can create disturbances which enhance the ability of *Postelsia* to recruit at a site. In Chapter IV, I examine the ecological factors which influence community structure in the wave exposed, *Postelsia* dominated understory algal community. I experimentally manipulated densities of the most common herbivore (*Lottia pelta*) and densities of *Postelsia* to examine the effects of

predation, competition and disturbance on the diversity and relative species abundances in the understory community. Finally, in Chapter V, I examine the results of my field experiments in a continuation of the discussion of the effects of water motion and wave-induced disturbance on intertidal macroalgae.

Chapter II

CAN WAVE FORCES LIMIT PLANT SIZES IN THE INTERTIDAL? AN EMPIRICAL TEST OF A BIOMECHANICAL MODEL

ABSTRACT

Plants that live in the intertidal zones of wave-swept shores are generally small relative to subtidal and terrestrial plants, and within a species, plants on wave-exposed shores are generally smaller than those at wave-protected sites. Wave forces have been proposed as a mechanism to account for limitations in size in the intertidal zone. The total in-line force on an organism in flow is the sum of the forces due to drag and acceleration, which are proportional to the area and volume of the organism, respectively. With increasing plant size, hydrodynamic forces increase faster than the plant's ability to maintain its attachment to the rock, thereby potentially limiting plant size in wave-exposed areas. Waves breaking onshore can produce flows with very high velocities and accelerations. Hydrodynamic forces generated by these breaking waves have been proposed as the primary physical factors limiting the maximal sizes to which wave-swept intertidal plants can grow. Until recently, major impediments to extending biomechanical models to algae have been (a) lack of adequate models to evaluate forces on flexible objects in flow; (b) lack of devices and models to measure and predict forces in surf zones; and (c) lack of reliable transplant techniques to experimentally test biomechanical models in the field. Of these impediments, (a) has been

addressed by Gaylord et al. (1994) and extended here, showing that algae experience large accelerational forces in oscillating flow which may effectively limit their maximal sizes, and I address (b) and (c) here.

The hypothesis that wave forces can limit plant sizes was extended to a population of *Fucus gardneri* at Fogarty Creek Point, OR in the following steps. I first constructed a mathematical model to predict the probabilities of survival for *Fucus* of various sizes under conditions of high and low wave exposure. I then calculated "optimal" sizes for *Fucus* under wave-exposed and wave-protected conditions where "optimal" sizes are sizes at which a plant has a maximal realized reproductive output. As a first evaluation of the model, I compared predictions to mean sizes of naturally occurring *Fucus* in both wave-exposed and wave-protected locations at different times of the year. Predicted optimal sizes of *Fucus* closely matched the mean observed sizes of plants collected from exposed and protected locations.

To test this hypothesis in the field, I reciprocally transplanted *Fucus* between wave-exposed and wave-protected sites and monitored maximum wave forces at each site as well as two plant variables, size and survival, over one year. I additionally tagged naturally occurring plants at both wave-exposed and wave-protected sites. Survival did not differ among transplants, transplant controls and naturally occurring tagged plants. However, significant differences occurred among treatments with respect to size. Mean sizes of wave-protected plants transplanted to exposed sites decreased significantly relative to protected control transplants. Mean sizes of wave-exposed plants transplanted to protected sites increased significantly relative to exposed control transplants. These results support

the hypothesis that wave forces have a direct influence on plant size in *Fucus,* and thus that wave forces can set mechanical limits to size in *Fucus.*

INTRODUCTION

Patterns of size in nature have long intrigued ecologists (Haldane 1928, Hutchinson and MacArthur 1960, Van Valen 1973, Marquet et al. 1990). Size distributions within populations of organisms may be influenced by competition as evidenced in populations of terrestrial plants (Obeid et al. 1967), marine invertebrates (Branch 1975, Menge 1972) and freshwater tadpoles (Wilbur and Collins 1973). Predation has also been identified as a strong factor influencing size and morphology in freshwater zooplankton (Brooks and Dodson 1965), marine mussels (Paine 1976a), and marine algae (Lubchenco and Cubit 1980, Lewis et al. 1987). Factors such as food availability, temperature, light, nutrient concentrations and reproductive status can all have important effects on the sizes to which organisms can grow (Sebens 1983). Organisms of different sizes are often found in very different physical environments (Schmidt-Nielson 1974, Peters 1983).

Maximum sizes of plants and animals in both terrestrial and subtidal marine environments are orders of magnitude larger than those of organisms in the zone between these two environments: the intertidal zone (Denny et al. 1985, Denny 1988, 1993a, Gaylord et al. 1994). Within this zone, the largest intertidal organisms on wave-swept shores are often much smaller than the largest intertidal organisms in more wave-protected habitats (Lewis 1968, Menge 1976). The following groups have been documented to have larger individual sizes on wave-exposed than protected shores: mussels and seastars (Harger 1970, 1972, Paine 1976 a,b), gastropods (Kitching 1966, Behrens 1972, Boulding 1990, Boulding and Van

Alstyne 1993), and seaweeds (Russell 1978, Schonbeck and Norton 1981, Norton 1991).

Why then are wave-swept organisms limited to such small sizes? The implication is that conditions in the wave exposed intertidal zone either curtail growth or break or remove organisms once they exceed a critical size. Water motion along wave-swept rocky shores produces some of the most powerful hydrodynamic forces on earth, and these forces on rocky shores may exert selective pressures for small size since hydrodynamic forces scale with organism size. Water velocities along an open coast may exceed 20 m/s and may be accompanied by accelerations greater than 1000 m/s^2 in storms (Denny 1988). These flows can impose tremendous forces on intertidal organisms. Due to the fact that seawater is approximately 800 times as dense as air, the force imposed on an intertidal organism by a flow of 20 m/s with accelerations of 1000 m/s^2 in seawater would be roughly equivalent to the force imposed on a similarly sized organism (assuming constant drag and inertia coefficients) in air by winds of 2015 km/hr and accelerations of 1.3×10^7 km/hr^2 (Denny 1990, 1993a). Based on these unrealistically high wind speed values, it seems unlikely that terrestrial organisms are ever limited in size due to wind forces. For wave-swept organisms, however, these conditions are real and present a common and serious challenge. Organisms living in these habitats must be able to withstand the hydrodynamic forces generated by large velocities and accelerations to survive and reproduce. Large organisms are more likely than small ones to be ripped off the rocks by waves, since hydrodynamic forces scale with size, and the idea that there are purely mechanical limits to the size to which organisms may grow is supported

for many groups of marine organisms: corals (Adey 1978, Chamberlain 1978, Highsmith 1980, 1982), mussels (Harger 1970, Paine and Levin 1981), kelps (Black 1976, Santelices et al. 1980), gastropods (Connell 1972, Boulding and VanAlstyne 1993) and intertidal invertebrates (Denny et al. 1985).

Denny et al. (1985) explored the possibility that wave forces could potentially set mechanical limits to size in wave-swept organisms. Their argument was based on the idea that hydrodynamic forces acting on organisms along wave-swept shores increase with increasing body size faster than the ability of the organism to maintain its attachment to the rock, thereby limiting the sizes of these organisms in wave exposed areas. Hydrodynamic forces that act on an object in flow are directly proportional to the size of the object and the velocity and acceleration of the fluid. Drag and lift are two important forces which act on objects in steady flow, both of which are proportional to the area of the object projected in flow. In addition to these forces, water motion in breaking waves produces a component of flow which is unsteady or accelerational; the *acceleration reaction* is an important additional force on organisms in an oscillating flow and is proportional to the volume of an organism. Total force on an organism in flow is the sum of the forces due to velocity and those due to the acceleration of the moving water. In isometrically growing organisms, volume tends to increase faster than area, thus accelerational forces can potentially set mechanical limits to size.

An organism's risk of dislodgement increases as the hydrodynamic forces which act to pull it from the rock become greater than its tenacity or ability to stay attached to the rock. Denny et al. (1985) constructed a

mathematical model to predict the probabilities that organisms of various sizes would survive under conditions of increasing wave exposure. For the limpets *Tectura (Notoacmaea) scutum* and *Lottia (Collisella) pelta,* the urchin *Strongylocentrotus purpuratus,* the mussel *Mytilus californianus* and the hydrocoral *Millepora complanata,* the model predicted that probability of dislodgement was increased substantially with an increase in size. Denny et al. (1985) did not apply their argument to wave-swept macroalgae. Seaweeds had been thought to escape significant accelerational forces due their flexibility and ability to re-orient rapidly in the direction of flow. However, Gaylord et al. (1994) found that some algae do experience large accelerational forces by effectively trapping water in their thalli. Using an oscillating flow tank, Gaylord et al. (1994) recorded significant accelerational forces for *Iridaea flaccida, Gigartina leptorhynchos* and *Pelvetiopsis limitata.* These species are common intertidal plants in California and represent a wide range of morphologies. In these species, accelerational forces in addition to drag may act as a size-dependent agent of mortality and effectively constrain the sizes at which algae survive and reproduce.

Seaweeds exhibit a great range of morphological variability within a species, particularly over gradients of wave exposure (Knight and Parke 1950, Burrows and Lodge 1951, Sideman and Mathieson 1983, Armstrong 1985, Norton 1991). Algae, unlike most land plants, are internally quite simple. Algae exhibit less specialization and differentiation of cell types and lack specialized tissues characteristic of land plants. Basically all parts of their thalli are involved in assimilation, absorption and secretion. They lack absorptive roots and nutrients are taken in over the entire surface.

There are many potential advantages to large size for an alga: Large plants may receive more sunlight, produce more spores or gametes, and may be less easily overgrown by neighboring plants or consumed by herbivores. The main disadvantage to large size in an alga is the higher probability of dislodgement by waves, since hydrodynamic forces increase with size. Plants that grow to large sizes must invest a higher percentage of energy in the production of structural tissues (such as large holdfasts and strong stipes) relative to their smaller counterparts, so that their overall ratio of photosynthetic to structural tissue is low. In general, the relative growth rate of larger plants is slower than smaller ones even under conditions of optimum resource availability (Norton 1991).

In addition to size, shape of a thallus potentially is an important determinant of the drag and accelerational forces on the plant. Carrington (1990) measured drag forces on thalli of *Mastocarpus papillatus* which varied in size and morphology. In this alga, drag force is primarily determined by the size of the thallus and is not strongly influenced by morphology. Young (1987) studied the hydrodynamic performance of *Fucus vesiculosus* and *Ascophyllum nodosum* and also found that plant size is more critical than plant shape in determining the drag force on the thallus. The findings that small size is more critical than a streamlined shape within a species for survival on wave-swept shores tend to correlate well with some observed patterns, i.e., that plants of similar morphology tend to be progressively smaller on more exposed shores (Norton et al. 1981).

In light of our understanding of the relationships between plant size and wave force in the laboratory and the observed difference in thallus size

across a range of velocities in nature, the question remains whether hydrodynamic forces are the mechanism responsible for these observed patterns of size with respect to exposure. I tested the hypotheses that wave forces set upper limits to plant size and that plant survival is dependent on plant size and the degree of wave exposure in a field study using the common brown alga *Fucus gardneri* (rockweed). The genus *Fucus* is well known for its great variation in morphology and size over exposure and tidal level gradients (Knight and Parke 1950, Schonbeck and Norton 1978, 1980, 1981).

In this study, I addressed the following questions:

1) Do wave forces mechanically constrain size to which *Fucus* can grow? Following the approaches of Denny et al. (1985) and Gaylord et al. (1994), I constructed a mathematical model to predict the probabilities of survival for *Fucus gardneri* of various sizes under conditions of high and low wave exposure. I calculated "optimal" sizes for *Fucus* under wave exposed and protected conditions ("optimal" sizes are sizes at which a plant has a maximal reproductive output as well as a reasonably high probability of survival). I then compared the predictions of this model to mean sizes of naturally occurring *Fucus* in both wave exposed and protected locations at different times of the year.

2) How are plant size and survival affected by wave exposure? I reciprocally transplanted *Fucus* between wave-exposed and protected areas and monitored maximum wave forces at each site and sizes and survival of all plants over a one-year period. I predicted that wave-exposed plants transplanted to wave-protected sites would have higher survival and/or greater increases in size relative to exposed control plants. I further

predicted that wave-protected plants transplanted to wave-exposed sites would have lower survival and/or would decrease in size relative to protected control plants.

Since both sites (wave-exposed and wave-protected) were within 100 m of each other and at the same effective tidal height, I assume that physical factors such as light, temperature and nutrient concentrations were similar between sites. Due to the greater water flows at the exposed site, nutrient exchange might actually be enhanced at this site and should result in faster growth at the wave-exposed site. Herbivores (snails and limpets) were more abundant at the wave-protected site and so any effects of grazing should be more intense at this site. Since I could not determine the plants' ages, I randomly chose reproductively mature individuals from each site.

METHODS

Study site

This study was conducted at Fogarty Creek Point, OR (FCP) (44° 51' N, 124° 03' W) 3.5 km north of Depoe Bay on the central Oregon coast. This site is a rocky (basalt) headland fully exposed to oceanic waves. Experimental plots were located on horizontal rock surfaces in the middle of the *Fucus* zone at both wave-exposed and wave-protected areas and ranged from 2.2-3.0 m above mean lower low water (MLLW). The high-zone, wave-exposed community at this site is dominated by *Fucus gardneri, Pelvetiopsis limitata, Mastocarpus papillatus, Endocladia muricata, Iridaea cornucopia* and the barnacles *Balanus glandula* and *Chthamalus dalli.* The most abundant herbivores are limpets *Lottia digitalis* and *Lottia strigatella* and the snail *Littorina scutulata.* The high-zone, wave-protected community is dominated by *F. gardneri* and *M. papillatus*,and *I. cornucopia* are occasionally present. The barnacles *B. glandula* and *C. dalli* are patchily present at this site and the snails *L. scutulata* and *Tegula funebralis* are the most abundant grazers. I will refer to all these species by genus in the remainder of the text.

Study organism - *Fucus gardneri*

Fucus gardneri is a common high intertidal brown alga in the order Fucales which occurs from Alaska to Pt. Conception, CA (Abbott and Hollenberg 1976). Species in this genus are extremely plastic in their

morphology (Knight and Parke 1950, Burrows and Lodge 1951, Powell 1957, Jordan and Vadas 1972) and the taxonomic status of *Fucus* species along the west coast of North America has recently been revised to include several varieties of *Fucus distichus* as *Fucus gardneri* Silva (Scagel et al. 1989). In this paper, I follow the opinion of Scagel et al. (1989) and consider the plants in this study to be *Fucus gardneri* and make no distinction among the subspecies. I refer in the rest of the text simply to '*Fucus*'. Voucher specimens were collected and pressed and are located at the Hatfield Marine Science Center Herbarium (Newport, OR).

The thallus of *Fucus* is attached by a broad discoid holdfast, from which arise bilaterally branched flattened fronds with a fairly distinct midrib. Receptacles are present at the apices of mature plants and become swollen at the time of reproduction. Fertile plants are found in the population throughout the year, but reproduction peaks slightly in the fall and winter (Ang 1991a). Plant growth is apical and branching is dichotomous. Reproductive structures (conceptacles) develop from cells in the swollen tips (receptacles) of higher order branches. The modular character of *Fucus* means that a single plant may be reproductive throughout the year as branches reach reproductive maturity at different times. *Fucus* are perennial and can reproduce for several years in a row (Ang 1991b). Reproduction takes place when plants reach their maximum size and plant growth rate is slowed due to reproduction (Ang 1992).

Fucus are very abundant in the high rocky intertidal area at FCP and are highly variable in size and morphology with respect to wave exposure. "Typical" wave-exposed plants tend to be short and have narrow blades and receptacles and resemble the related fucoid *Pelvetiopsis limitata*, while

"typical" wave-protected plants have a much larger thallus with wider blades and receptacles (Fig. II.3). Plants used in this study were reproductively mature and were randomly chosen from the middle of the *Fucus* zone at both areas of wave exposure to avoid any confounding effects of tidal height on plant size and morphology.

Wave force measurement

I chose wave-exposed and wave-protected sites within Fogarty Creek Point (hereafter FCP) after observing the intensity of wave spray caused by breaking waves in several areas (Fig. II.1). The more seaward, wave-exposed site was located near patches of the sea palm *Postelsia palmaeformis*, considered by many intertidal ecologists to be a biological indicator of high wave exposure. The more landward wave-protected site was dominated by large *Fucus* plants. To quantify the relative wave intensity, I installed maximum wave force meters at both sites. Maximum wave force meters are designed to record the force imposed by the largest wave passing over the device during the time of deployment. The maximum wave force meters were developed by Bell and Denny (1994) and the spring tensions and attachment system have been slightly modified for use at FCP. The device (Fig. II.2) consists of a wiffle golf ball attached via braided dacron fishing line (80-130 lb. test) to a stainless steel spring (Associated Spring :E0360-058-3000S for wave-exposed areas and E0360-055-3000S for wave-protected areas). The spring was housed in a 6.5 inch by 0.5 inch section of CPVC plastic, the ends of which were fitted with sections of 0.5 inch (molybdenum filled) nylon rod and 0.5 inch delrin rod.

Like the devices used by Jones and Demetropoulus (1968), the wiffle ball acts as a drogue upon which the waves pull. Maximum force is recorded by measuring the displacement distance of a rubber slider fitted on the braided dacron fishing line between the spring and the nylon molybdenum end. Each meter was calibrated in the laboratory by measuring the displacement distance of the rubber slider using known weights suspended from the wiffle ball end. Each wave force meter was deployed in the field by attaching a large stainless steel swivel (Berkely 1500 lb, size 10/0) to the delrin end of the meter using nylon machine bolts and nuts (Small Parts Inc.). Large 3/8 inch stainless steel eyebolts (Tacoma Screw) were installed at several locations in both wave-exposed and protected areas at Fogarty Creek Point. Small (3/16 inch) stainless steel quick-links (Seattle Marine) were used to attach wave force meters to eyebolts and provided a secure and easy method for attaching and removing the meters. Several wave force meters (usually between 3-10) were deployed at each area during each sampling date. Meters were recovered after 24 hours and measurements were recorded. Wave force meters were not deployed during extremely large winter storms to avoid losses of devices. Recordings from meters that lost their (wiffle) balls, became snagged, or were deployed for longer than one day were not included in analyses.

Breaking strength

Breaking forces were measured for *Fucus* individuals collected at FCP. One hundred plants were collected from both wave-exposed and wave-protected sites at FCP. I sampled plants at FCP in March and August

1992 and February 1993. The exposed and protected sites at FCP were 100 m apart (as the seagull flies). I placed a 10 m transect in the middle of the *Fucus* zone at each site and randomly sampled ten mature (reproductive) plants from a 0.25 m^2 quadrat placed at each meter along the transect.

The breaking force for each plant was determined using the method of Carrington (1990) and Gaylord et al. (1994). One end of a short length of string was tied to a 5000 g spring scale (Ohaus, modified to record maximum force using a rubber slider), and the other end formed a noose which was placed around the stipe (near the holdfast) of the plant. The spring scale was pulled parallel to the substratum in a constant manner simulating a constant hydrodynamic force, until the thallus either detached from the rock or broke. The force required to induce this mechanical failure (maximal force) was then recorded to the nearest 1 N (N=newton).

Length of each plant (L) was measured from the holdfast to the tip of the longest branch. I determined the maximal projected area (A) of each plant (planform area) by photographing each individual and measuring plant area using an image processing program (Image 1.41, National Institute of Health). Each plant was weighed to the nearest 0.01 g after being shaken dry and blotted to remove excess water. Since the density of the algal material was assumed to differ little from seawater (Gaylord et al. 1994), algal volumes were approximated by dividing masses (kg) by the density of seawater (1025 kg/m^3).

Model and data analysis

Data on variation in algal strength were analyzed as in Gaylord et al. (1994). I fit a power curve to the model relationship between plant area (A) and maximum force (force at which plant was dislodged) for *Fucus* from each date (March and August 1992; February 1993):

$$\text{Force} = x + y\,A^{z} \qquad (1)$$

where x, y and z are constants fit to the power curve for each date using a non-linear, simplex, iterative procedure (Wilkinson 1990) (Table II.1). Force to break each individual thallus was then expressed as the ratio (f') of its measured breaking force to the breaking force predicted by the regression of the Force/Area relationship. Variation in this relative breaking force provides a means of estimating the probability that a plant chosen at random will have a strength exceeding a given value. Relative breaking forces were ranked in ascending order (lowest relative force having rank 1) and the probability P of having a relative breaking force less than that of the plant with rank j was estimated as:

$$P = j / (N + 1) \qquad (2)$$

where N is the total number of plants tested. This cumulative probability distribution was described mathematically using a modified Weibull model fit to the probability data by a maximum likelihood, non-linear,

iterative estimate (Wilkinson 1990, Denny and Gaines 1990, Gaines and Denny 1994):

$$\underline{P(f')} = \exp - \{[(a-b\underline{f'})/(a-be)]^{1/b}\} \quad (3)$$

where a, b and e are constants determined derived from the estimation procedure. (Table II.2). This distribution describes the probability $\underline{P}$ that a given relative breaking force is less than a value $\underline{f'}$.

I followed the approach of Gaylord et al. (1994) in developing a model that predicts the probability that a plant will survive (i.e., not be dislodged) in a 3 month period as a function of: the plant's size, the force required to dislodge the plant, the maximum velocities and accelerations typical of its home site, and the probabilities of encountering waves with the given flow parameters. Based on empirical data (Denny and Gaines 1990, Denny 1991, 1993b,c), **predicted maximal force** ($\underline{F}_{max}$) imposed on a wave swept organism is the sum of forces due to both **drag** and the **acceleration reaction**:

$$\textbf{Drag} = [(1/4)\,(\underline{M}_{y,max})^2(\underline{H}_m)^2\,\underline{p}\,\underline{C}_d\,\underline{A}] \quad (4)$$

$$\textbf{Acceleration Reaction} = [\underline{C}_m\,\underline{p}\,\underline{V}\,\underline{a}] \quad (5)$$

$$\underline{F}_{max} = \textbf{Drag} + \textbf{Acceleration Reaction} \quad (6)$$

where $\underline{M}_{y,max}$ is the ratio of the predicted maximal wave height to the mean significant wave height, $\underline{H}_m$, a measure of the average "waviness" of the ocean at a particular site (Denny 1988, 1991, 1993b,c, Gaylord et al. 1994). The shape of the distribution of mean significant wave heights is

similar among sites on the west coast of North America (Denny 1991,1993b). $M_{y,max}$ for a period of 3 months is approximately 5.5, so that in a 3 month period, the highest wave present offshore at a site is likely to be about 5.5 times the mean significant wave height at that site for that period. C_d and C_m are the empirically determined drag and inertia coefficients of *Fucus* (0.15 and 8.00), as measured by Brian Gaylord (Hopkins Marine Station, Stanford University) using a method similar to that used by Daniel (1985). ρ is the density of seawater (1025 kg/m^3), a is the acceleration imparted by the breaking wave and V is the plants' volume which can be expressed as an allometric function of A:

$$V = f A^g \tag{7}$$

where f and g are coefficients determined by a least squares fit to the volume-area data, calculated using a simplex algorithm applied to the untransformed data (Wilkinson 1990) (Table II.3). This allows the probability of survival to be represented as a function solely of plant area.

Probability of survival

Following the approach of Gaylord et al. (1994), I used the above relationships to estimate the probabilities that *Fucus* plants of different thallus areas growing along wave-exposed and wave-protected shores could survive (i.e., not be dislodged) over a three month time period (i.e., a seasonal probability of survival). Thus, probability of survival in this model is equivalent to the probability that a plant will not be dislodged by

waves in a given time period and is based solely on biomechanical factors, ignoring other biological and ecological factors (i.e., grazing, desiccation, shading). I estimated the wave-protected site at FCP as having a mean significant wave height of 1 m ($\underline{H}_m$=1 m, a typical yearly value for a moderately protected site) and the wave-exposed site an $\underline{H}_m$=2 m (a typical yearly value for an exposed site). At present there is no method for estimating the acceleration that accompanies a given velocity in a breaking wave. I followed the approach of Denny et al. (1985) and Gaylord et al. (1994) and specified a reasonable range of accelerations based on available measurements of velocity and wave exposure made by Denny et al. (1985) at Tatoosh Island, WA.

Reproductive output and optimal size

The number of gametes (eggs and sperm) that any individual *Fucus* plant can produce can be modeled as being proportional to the individual's volume. Mean reproductive biomass of a *Fucus* plant over a year comprises approximately 12.7% of the total plant weight (Ang 1992), thus reproductive output of a plant is directly proportional to volume. Theoretically, an individual should grow as large as possible to maximize reproductive output. However, as an individual grows large, forces acting on the plant due to the velocity and acceleration of the moving water increase as well, with drag increasing proportionally to area, and acceleration reaction increasing proportionally with volume. There is a tradeoff between survival and growth to reproduction in which an individual should grow large to increase reproductive output, but not so

large that it risks becoming dislodged. Ignoring perennation and vegetative propagation due to fragmentation, Denny et al. (1985) and Gaylord et al. (1994) defined an index of the realized reproductive output (IRO) of an individual as the product of plant volume ($\underline{V}$) and the probability that the individual will survive intact to the time of reproduction ($\underline{P_S}$) over a specified time period.

$$IRO = \underline{V}\,\underline{P_S} \tag{8}$$

This model allows prediction of an optimal size at which the plant has a maximal reproductive output.

RECIPROCAL TRANSPLANTS

Experimental design

I chose a wave-exposed and a wave-protected site at FCP for a reciprocal transplant experiment based on wave observations and wave force meter recordings. At each site, I placed a 10 m transect in the middle of the *Fucus* zone and chose ten mature (reproductive) plants from a 0.25 m^2 quadrat placed at each meter along the transect. I carefully chiseled out a solid section of the rock from beneath the holdfast of each chosen plant. Plants were only used in the transplant experiment if the adhesion of the holdfast to the section of rock remained firm during this process. I continued sampling until I had collected 120 plants from each area. The transplant technique involved gluing the sections of rock to which plants

were attached into pre-chiseled holes at the transplant site using marine epoxy putty (Z spar, Kopper's Co. Los Angeles) so that the transplant was flush with the surrounding rock (Fig. II.4). The advantages of this technique are that the plant's tenacity to the rock is maintained and the epoxy does not touch the plant or interfere with its growth. Each plant was individually marked by attaching a numbered plastic label to the marine epoxy putty.

The experimental design consisted of 60 wave-exposed plants transplanted to the wave-protected area (E to P) and 60 wave-protected plants transplanted to the wave-exposed area (P to E). Likewise, 60 wave-protected plants were transplanted back to the wave-protected area (P to P) and 60 wave-exposed plants were transplanted back to the wave-exposed area (E to E). These latter transplants served as controls for the transplant procedure. In addition to the control plants, 60 mature randomly chosen, naturally occurring, unmanipulated plants were identified at each site. I identified them by placing a marine epoxy spot with a numbered plastic label and arrow near the holdfast of the plant.

Data collection

The transplant experiment was initiated in September 1992 and lasted one year. I censused the transplants and controls each month. For each individual I recorded survival, size (length and planform area) and approximate reproductive status. Since *Fucus* plants can perennate and regrow from a holdfast, I recorded plants as missing only when the entire holdfast was dislodged. I measured length by measuring the length of the

longest branch. I measured planform area by photographing each individual against a white sheet next to a ruler and then analyzed the area of the plant in each photograph using an image analysis system ("Image"). Counting the number of reproductive blades on each plant was not logistically possible due to time limitations and so I used a subjective measure of reproduction. For each plant I determined if many (scored as 3), some (= 2) or few (= 1) blades on each plant beared reproductively mature receptacles. With the exception of the wave-exposed plants in winter, I measured survival and length of the longest branch of the unmanipulated tagged plants each month.

Data analysis

Fucus size/strength data and wave force meter data were analyzed using a two way analysis of variance (ANOVA) to determine the effects of date and wave exposure on each of the variables. To meet the assumptions of normality and variance homogeneity, data were log-transformed. Survival data were analyzed using a Logrank test (Hutchings et al. 1991) to compare the proportional survival of plants between the treatments and controls, and between controls and tagged plants. Repeated measures ANOVA on log transformed data was employed to evaluate treatment effects on algal area and length over the one year period. Seasonal variation in maximum plant size was evaluated using ANOVA. Seasonal maximum sizes were determined by grouping data from September, October and November (fall), December, January and February (winter), March, April and May (spring) and June, July and August

(summer) to reduce the number of comparisons. Comparisons of mean changes in length and area of plants surviving the entire experiment were done using a Mann-Whitney U test since sample sizes were small ($n<8$) and variances non-homogeneous (Bartlett's test). I compared the reproductive status of transplants and controls between wave-exposed and wave-protected sites over the one year period using a two-way ANOVA.

Plastic plant transplant

To observe the effects of wave exposure on the size of a non-biological "plant", I transplanted three plastic aquarium plants to both the wave-exposed and the wave-protected site on March 31, 1994. The sizes of plastic plants are not affected by competition, herbivory, nutrient or light levels, and so any site differences in terms of the changes in the sizes of these plants should be directly attributable to the differences in physical flow forces between the two sites. Each plastic plant was manufactured to represent the freshwater plant *Cardamine lyrata* (Penn-Plax Plastics, Garden City, NY) and reasonably resembled (in terms of both size and shape) an average, wave-protected *Fucus*. Each plant was approximately 16 cm tall and had 7 fronds which attached to the central axis near the base. I attached the plants at each site using the *Fucus* transplant technique described above. I attached the base of each plant allowing each of the fronds to be exposed to water flow, and quantified the number of branches remaining on each plant at 2 and 4 days following the transplant.

RESULTS

Size and breaking strength distributions

Mean sizes (areas, lengths, weights) of *Fucus* plants from wave-exposed areas at all dates and at all locations were significantly larger than those from wave-protected areas (Fig. II.5). For area, length and weight, a two way ANOVA showed the effects of date and exposure to be highly significant (both $p<0.001$) and the effects of wave exposure varied, depending on the month (significant date x exposure effects) (Table II.4). Areas and weights of plants were greater in the summer month than the winter months. Protected plant lengths were greatest in February 1993. The breaking strengths of wave-exposed plants were significantly greater than those of wave-protected plants, but there was no significant interaction between date and exposure ($p=0.1675$) (Fig. II.6). Breaking strength was measured as the force required to dislodge a plant divided by the cross-sectional area of the break. Thus although *Fucus* were larger at the wave-protected site, mean *Fucus* strength was greater at the wave-exposed site.

Probability of survival

Model results indicate that probability of survival decreases as both plant size and wave exposure increase (i.e. with larger values of acceleration) (Fig. II.7). The model predicts that wave-exposed plants, normally small, should have a very high probability of survival under

wave-protected conditions (low velocities and accelerations) and would have only a slight risk of dislodgment by waves at their mean observed sizes. In contrast, wave-protected plants should have very low probabilities of survival under wave-exposed conditions (high velocities and accelerations) and experience almost certain dislodgment by waves at their mean observed sizes (Fig. II.5). Wave-exposed plants at wave-exposed sites have a 30%-80% probability of survival and wave-protected plants at wave-protected sites have a 10%-90% probability of survival depending on the degree of waviness (in terms of acceleration and velocity) and the time of year. Sites are likely to experience larger accelerational forces in the winter months (March and February) when weather patterns produce frequent storms than in August when wave conditions are generally calm (Figs. II.9, II.10 & II.12). In this model accelerations of 100-200 m/s^2 might be typical for wave-protected sites in summer and accelerations of 200-300 m/s^2 might be typical for wave-protected sites in winter. Likewise wave-exposed sites should experience lower accelerations in summer (500-600 m/s^2) than in winter (600-700 m/s^2).

Index of reproductive output

Index of reproductive output is used only as a relative measure, since it does not represent a precise measure of a plant's actual reproductive capacity. The utility of the concept is that it provides a means to examine the tradeoffs between growth and survival. In all cases, predicted reproductive output increases with an increase in plant area, but only up to a certain size (Fig. II.8). Above this size, low probability of

survival due to drag begins to offset the increase in the number of gametes that can be produced, and reproductive output declines. The optimal size in this sense is the size at which the plant has a maximal realized reproductive output.

In all cases, observed sizes of *Fucus* lie within or close to the optimal sizes predicted by the model using values of acceleration appropriate for time of year as described above (Table II.5). In March, for example, the mean observed size of wave-protected *Fucus* (A=0.0040 m^2) at the protected site with estimated accelerations of 200-300 m/s^2 falls in the predicted optimal size range of 0.0047 m^2 to 0.0034 m^2. Similarly, the mean observed size of wave-exposed *Fucus* (A=0.0010 m^2) at the exposed site with accelerations of 600-700 m/s^2 lies within the predicted optimal size range of 0.0011 m^2 to 0.0008 m^2.

Wave forces

Maximum wave force meters provided evidence that the wave-exposed area experienced forces that were 2 to 4 times as great as forces in the wave-protected area. Maximum wave forces were consistently larger at wave-exposed areas than at wave-protected areas over the course of the study (one way ANOVA effect of exposure $p<0.001$) (Fig. II.9). These wave force measurements are actually an underestimate of the maximum wave forces at each site since the measurements were made on only one or a few days per month, and wave force meters were not deployed during large winter storms, since the site was inaccessible during these times.

Although I have only measured wave forces at FCP on a few days per month it is possible to estimate the magnitude of wave forces at the wave-exposed FCP site using wave height measurements from an offshore buoy (NDBC #46040: 44.8° N, 124.3° W) (Fig. II.10) that is located approximately 60 km offshore from FCP. This buoy provides average monthly mean ($\underline{H_m}$) and maximum ($\underline{H_{max}}$) significant wave heights, but does not provide daily data. Another offshore buoy (National Weather Service buoy #50: 44.6° N, 124.5° W) is located approximately 145 km offshore from FCP and provides mean significant wave heights every three hours. There is a significant correlation between maximum wave force measured at the wave-exposed area of FCP and predicted wave force calculated using the maximum, mean significant wave height from buoy #50 over the same period that the wave meter was deployed (Fig. II.11). The mean predicted wave force ($\underline{F_m}$) on a wave-exposed maximum wave force meter can be calculated as follows (see also Denny and Gaines 1990, Denny 1991):

$$\underline{F_m} = \{0.5\ \underline{\rho}\ \underline{A}\ \underline{C_d}\ [2\ (9.81\ \underline{H_m})]\} + [\underline{C_m}\ \underline{\rho}\ \underline{V}\ (100\ \underline{H_m})] \qquad (7)$$

where $\underline{\rho}$ is the density of seawater, $\underline{A}$ and $\underline{V}$ are the area and volume of the maximum wave force meter wiffle ball, $\underline{C_d}$ and $\underline{C_m}$ are the empirically determined drag and inertia coefficients for the tethered wiffle ball (Gaylord et al. 1994). As mentioned earlier, there are currently no simple and reliable methods for measuring the acceleration of the water in a given wave. Based on the few empirical measurements that have been made (Denny et al. 1985) acceleration values (in m/s^2) for waves onshore are

approximately 100 times the mean significant wave heights (in m) (see Denny 1993). This is obviously a crude approximation and the values of mean predicted wave force should also only be viewed in an approximate sense. Maximum wave force over the month can be calculated using equation 7, and replacing $\underline{H_m}$ with $\underline{H_{max}}$ for that month. Monthly mean and maximum predicted wave forces for 1988, 1989, 1990 and 1991 are shown in Figure 12 (data are not available from buoy #46040 after 1991). This procedure allows one to estimate the monthly mean and maximum wave forces that wave-exposed organisms are likely to experience.

TRANSPLANT EXPERIMENT

In the remainder of the text, the protected plants transplanted to exposed sites will be referred to as "P to E", exposed plants transplanted to protected sites as "E to P", protected plants transplanted to protected sites as "P to P" and exposed plants transplanted to exposed sites as "E to E".

Survival

"Percent survival" was measured as the number of plants remaining in each treatment each month (x 100) divided by the number of plants in each treatment at the start of the experiment. In cases where plants disappeared, the holdfast of the plant was no longer present on the rock. The marine epoxy putty and tag did not dislodge in any cases. The number of plants remaining in each treatment steadily declined over the course of the experiment (Figs. II.13 & II.14) (I was not able to sample the

exposed control plants in the winter months due to lack of adequate low tide time during stormy periods). I calculated Log-rank statistics to determine if percent survival differed over the course of the experiment between treatments and controls and between controls and tagged plants (Table II.6 a-d). In all cases the percent survival did not significantly differ over the course of the experiment between the treatments and the controls or between the controls and the tagged plants. There were no significant relationships between size and survival in any of the treatments or controls.

Size

Mean planform areas of P to P slowly increased over the course of the experiment. Mean planform areas of P to E sharply decreased, however, especially during the first few months of the experiment (Fig. II.15). Mean planform areas of P to E were significantly smaller than those of P to P over the course of the experiment (Table II.7). The mean planform areas of E to E decreased gradually over the course of the experiment (fall and winter). Mean planform areas of E to P increased over the course of the experiment, particularly during spring and summer. There were significant changes in area over the course of the experiment in exposed plants due to the transplant. The mean planform areas of plants became larger than E to E over the course of the experiment. Patterns for changes in length were similar to those for area (Fig. II.16). Lengths of P to E became smaller than P to P over time, while lengths of E to P became larger than E to E over time. There were significant differences

in length between the transplants and controls over the experimental period (Table II.8).

If wave forces are important in limiting size, waves should prune or dislodge the largest plants. Maximum plant area is equal to the area of the largest plant in each treatment during each month. However, maximum area was relatively constant in both P to P and E to E (Fig. II.17). Maximum areas of P to E dropped sharply in the first few months of the experiment. This was due mainly to large plants losing branches and area to waves, and also to plants of all sizes becoming dislodged. Maximum sizes of P to E slowly converged on the maximum sizes of naturally occurring exposed plants. Maximum sizes of E to P increased slowly over the course of the experiment due to plant growth. The maximum areas of P to E became smaller than P to P controls over the course of the experiment, and maximum areas of E to P became larger than E to E controls (Table II.9). Patterns for maximum plant lengths were similar in their trends to patterns of area (Fig. II.17). Maximum lengths of P to E became smaller than P to P over time while maximum lengths of E to P became larger than E to E over time (Table II.10).

Mean and maximum lengths of both P to P and E to E did not differ from mean and maximum lengths of naturally occurring protected and exposed tagged plants suggesting that the transplant controls were appropriate mimics of naturally occurring protected plants (Fig. II.18). Although plant sizes in all treatments varied over time, there were no significant treatment or treatment x date interactions in the comparison of mean lengths of P to P and protected tagged plants and in the comparison of mean lengths of E to E and exposed tagged plants (Table II.11). There

also were no significant treatment or treatment x date interactions in the comparison of maximum lengths of P to P and protected tagged plants and in the comparison of maximum lengths of E to E and exposed tagged plants (Table II.12).

Mean absolute change in size (in terms of both area and length) of plants which survived more than eight months of the experiment was greatest in P to E (Fig. II.19). P to P increased in size (area and length), while E to E slightly decreased in area, yet did not change significantly in length. E to P gained in size (both area and length) over the experiment. Mean changes in area and length between P to E and P to P were significant (Mann-Whitney U = 63.000, $p<0.001$; Mann-Whitney U = 0.000, $p=0.002$) as were the mean changes in area and length between E to P and E to E plants (Mann-Whitney U = 5.000, $p<0.001$; Mann-Whitney U = 26.000, $p=0.016$).

Reproductive status

P to E retained significantly fewer reproductive blades per thallus over the experiment than did P to P (Table II.II.13, Fig. II.20). E to P contained significantly more reproductive blades per thallus for most of the experiment than did E to E.

Plastic plants

All three plastic plants at the wave-exposed site lost all their branches within 4 days, while only one of the three plants at the wave protected site lost any branches over nearly a two month period (Table II.14).

DISCUSSION

The relationship between size and wave exposure

Many studies of intertidal seaweeds have documented the general trend of decreasing thallus size with increasing wave exposure in such diverse taxa as *Callithamnion* spp. (Price 1978), *Chondrus crispus* (Mathieson and Prince 1973, Dudgeon and Johnson 1992), *Corallina officinalis* (Dommasnes 1968), *Fucus* spp. (Burrows and Lodge 1951, Russell 1978) *Zonaria farlowii* (Dahl 1971), *Ulva fasciate* (Mshigeni and Kajumulo 1979), *Ulva lactuca* (Steffensen 1976), *Ascophylum nodosum* (McEachreon and Thomas 1987) and *Sargassum cymosum* (De Paula and De Oliveira 1982). Intraspecific variations in size and morphology have also been documented in freshwater plants inhabiting streams at different flow regimes with the smallest, most turfy plants growing in the fastest flow areas (Sheath and Hambrook 1988, Brewer and Parker 1990, Chambers et al. 1991).

Sizes of *Fucus gardneri* on the Oregon coast follow this pattern of increasing size with decreasing wave exposure. My experiments suggest that size is affected by the degree of wave-exposure within a single site at the same tidal level. *Fucus* vary in morphology as well as in size along this wave exposure gradient. Wave-protected plants have wider and thicker blades than wave-exposed plants (personal observation). This pattern is also common in other species of *Fucus*. Sideman and Mathieson (1985) showed that variation in morphology of *Fucus distichus* with respect to wave-exposure was maintained when the progeny of the *Fucus*

morphs were grown in an experimental garden. Sideman and Mathieson (1983) outplanted laboratory cultured plants from different *Fucus* morphologies to a common garden site and found that morphology of the transplant was correlated to that of a parent plant, suggesting that the morphological variation in *Fucus* may have a genetic component. Although I have presented evidence that wave exposure can affect the sizes of *Fucus*, I have no evidence for changes in morphology (i.e., blade width) and so it may be likely that variations in plant morphology are genetically based.

Investigators studying the effects of water motion on plant form have been plagued by two major difficulties: the lack of an adequate transplant technique and the difficulty of measuring wave exposure in any but a subjective or relative manner (Norton et al. 1981). Transplants of seaweeds in the field have been made by moving boulders with attached plants in the case of *Fucus* (Pollock 1969, Schonbeck and Norton 1981, Chapman and Johnson 1990) and *Sargassum* (De Paula and De Oliveira 1982). Transplants of wave-protected plants to wave-exposed locations have not been successful, since large waves remove entire rocks which are not carefully secured at wave-exposed sites. The transplant technique used in this study proved highly reliable. Although chiseling the rock from beneath the holdfast of the plant requires some practice and much patience and time, the rock to rock adhesion made using marine epoxy putty worked well and never failed in hundreds of transplants.

Previous studies of algal morphology have attempted to measure the degree of wave exposure by estimating wind direction, fetch length or by making subjective estimates of the general waviness. Even assessments

of relative exposure may depend on the experience of the investigator and the tolerance of the species under investigation. While wave-exposed and wave-protected were used in relative terms, I have actually quantified the maximal forces that may be experienced by a *Fucus* plant at each site by using maximum wave force meters. Maximum wave force is an appropriate measure since the maximum size to which an organism can safely grow is in large part a function of the force caused by the most extreme wave that the organism can be expected to experience. On all dates for which I had measurements, the wave-exposed area experiences significantly larger maximum wave forces than the wave-protected area. While there are no simple methods to estimate accelerations accompanying a given velocity in a breaking wave, it is possible to specify a reasonable range of accelerations based on previous empirical measurements (Denny et al. 1985, Gaylord et al. 1994). Wave-swept organisms are likely to encounter water flows in breaking waves in the form of turbulent bores. When an organism in the intertidal zone encounters this onrush of moving water, accelerations are likely to be quite large and flows may be best described as turbulent. Denny et al. (1985) recorded accelerations in the surf zone of Tatoosh Island, WA in excess of 400 m/s^2. Since these recordings were made during relatively calm conditions, Denny et al. (1985) estimated that accelerations as high as 1000-2000 m/s^2 may occur during winter storms. These accelerations are relative to rigid objects firmly attached to the rock. Algae which are flexible are likely to experience lower effective accelerations (Koehl 1984). Since wave forces at Fogarty Creek Point, OR are likely to be similar to those at Tatoosh Island, WA, I specified values of accelerations from 100-700 m/s^2

in model predictions. These are slightly higher than values used by Gaylord et al. (1994) for algae on the central California coast since the degree of wave exposure at FCP is probably greater than that at the California sites used by Gaylord et al. (1994) (personal observation).

ASSUMPTIONS AND LIMITATIONS OF THE MODEL

The model used in this paper is similar to that developed in Gaylord et al. (1994), in which several simplifying assumptions contained in the model are explained more fully. Briefly, these assumptions are that (1) inertia coefficients measured in the lab approximate those in surf zone conditions, (2) plants will become dislodged at the holdfast when they encounter the predicted maximal force, and (3) reproductive output is directly proportional to plant volume.

Reorientation in flow and variable inertia coefficients

Drag and inertia coefficients used in the model in this study were measured in the same oscillatory flow tank used in the Gaylord et al. (1994) study, where problems in interpreting algal inertia coefficients were thoroughly described. The greatest difficulty in determining Cd's and Cm's of algae in unsteady flow results from the variation in algal shape as velocities and accelerations change. Gaylord et al. (1994) mimicked this behavior by measuring drag and inertia coefficients on a fixed wiffle ball and on a tethered wiffle ball that was allowed to move and reorient as the fluid accelerated and decelerated. The inertia coefficients for the tethered

wiffle were lower than those for the fixed wiffle, however the tethered wiffle still experienced relatively large accelerational forces. Although the consequences of this behavior are still not fully understood, Gaylord et al. (1994) suggest that the Cd's and Cm's measured in the oscillating flow tank are reasonable approximations of drag and inertia coefficients of *Fucus* in surf zone flows.

Probability of survival model

The model predicting probability of survival is based on the distribution of measured breaking forces to relative breaking forces and provides a means of estimating the probability that a plant chosen at random will have a strength exceeding a given value. The function describes the probability that a plant of a given size will experience a force that is less than the maximum force required to dislodge the plant from the rock. This model assumes that a force above this maximal force will rip the entire plant from the rock and that any force below this maximal force will leave the entire plant intact. The model fails to account for thallus tattering, when individual blades or sections of the thallus are removed by waves while the holdfast remains attached to the rock. The cross-sectional area of a branch is usually less than that at the stipe or holdfast, so plants should break at these points at a lesser force than is required to dislodge the entire thallus. A sub-lethal force may break off several branches of a plant reducing its overall area and volume. In this case, the plant's probability of survival is increased, since the area of the plant is reduced while its tenacity remains unaffected. As evidenced in the

transplant experiment, thallus tattering is common and seems to be an important method of size reduction (personal observation).

Reproductive output and optimal size model

The primary assumption in the model of reproductive output versus plant size is that the number of gametes that a plant can produce in a given amount of time can be modeled as being proportional to plant volume. This seems a reasonable approximation in *Fucus* since larger plants bear larger receptacles (personal observation), although I have no data on how the number of eggs and sperm per receptacle scale with receptacle size. Ang (1992) found that the reproductive biomass of *Fucus distichus* was approximately 12.7% of the plant dry weight and this value was relatively constant over most months. Vernet and Harper (1980) estimated that the eggs of various species of *Fucus* account for 0.1% to 0.4% of the plant's total weight. In this simple scenario where the optimal plant size is the product of volume and the probability of survival over a season, mean observed plant sizes from all dates and exposures at FCP fit the model predictions very well. Since I have not directly measured accelerations at each site, these calculations based on optimal size are rather preliminary. However, the correspondence of the predicted optimal sizes to the mean observed sizes suggests that wave forces may be important factors influencing size in *Fucus*.

OTHER FACTORS AFFECTING PLANT SIZE

The mechanical behavior of an alga depends on its gross and microscopic morphology. In general, macroalgae have low stiffness and strength, and high extensibility when compared to many other biomaterials (Koehl and Wainwright 1977, Koehl 1979, 1986, Denny et al. 1989). The high degree of flexibility and extensibility of intertidal seaweeds provides shock absorption which may prevent complete dislodgment at sites subjected to short pulses of high water motion. Although the stipes of brown algae lack woody tissues, some genera, such as *Fucus*, produce an inner core or medullary network consisting in part of very rigid, parallel aligned fibers that provide strength. The bulk of this inner core is increased from year to year by cellular division (Niklas 1992).

Regardless of an alga's material properties, a plant may be dislodged from the substratum if the adhesion of its holdfast to the substratum fails. Some seaweeds such as *Postelsia palmaeformis* are detached when the rock, mussel, alga or barnacle to which they are attached breaks free or dies (Dayton 1973, Paine 1979, 1988). Once the adhesive strength of the organism exceeds that of the rock or other organisms to which it is stuck, the organism cannot effectively increase its ability to stay attached to the shore by a further increase in strength. In these instances the strength of the rock limits the ability of the organism to withstand waves. In several instances, while measuring breaking strengths of *Fucus* at FCP, the rock beneath the holdfast gave way before the plant broke.

Seasonal variation in wave exposure can also affect plant size. Plants with annual life histories can take advantage of a lull in wave action

during summer to grow and reproduce. *Nereocystis luetkeana* and *Postelsia palmaeformis* are annual kelps which attain very large sizes in summer, and are usually ripped from the rock by heavy wave action in winter. Perennial plants, such as *Fucus*, have meristems that remain totipotent and are able to adjust the plant's form to adapt to prevailing conditions (Norton 1991). A plant that grows beyond the optimum size during an extended calm period, such as in summer, may be pruned back to a more sustainable size in a subsequent storm. This strategy, apparent in *Fucus*, allows a plant to grow continually and reach a very large size/reproductive output during calm periods. Plant sizes in summer, during periods of low waves are considerably larger than in March or February during large wave, stormy periods (Fig. II.3).

Vegetative propagation and perennation serve as important reproductive strategies in seaweeds (Cheney and Mathieson 1978). Fracture may be a useful mechanism of asexual reproduction and spore dispersal. Broken-off fragments may contain spores, conceptacles or gametes or may be able to re-attach to the substratum and grow (Norton et al. 1982). Fracture may be a mechanism of dispersal in seaweeds such as *Fucus* which contain bladders or receptacles that float in seawater, similar to the findings of Paine (1988) that floating *Postelsia* may act as agents of long-distance dispersal. Breakage at branch points of reproductively mature receptacles would produce long distance dispersing rafts of gametes. Although this non-lethal pruning might account for some reproductive success in *Fucus*, this possibility has been ignored in the predictions of optimal size.

It is possible that biomechanical factors and the ability of seaweeds to break and loose large portions of their thalli may partially help to explain why "simple" plants like algae are more successful in wave-swept intertidal areas than "higher" or more "advanced" vascular plants (Lubchenco, personal communication). During winter storms, intertidal plants are likely to tatter and rip and it may be advantageous to have less specialization and differentiation and therefore more "flexibility" in continuing to function after a period of large waves and potentially large tissue loss.

Biological constraints on plant size

For many organisms, age is highly correlated with size. This is true for organisms with determinate growth (many vertebrates). Many invertebrates and seaweeds are indeterminate growers, and there is often little or no relationship between size and age. Seaweeds may be constantly pruned by waves over the course of their lifetime and actually decrease in size as they get older. There is no known, reliable method for determining the age of a given specimen of *Fucus*. Ang (1991a) followed size, growth and mortality of a cohort of *Fucus distichus* in Vancouver, B.C. and found that size of *Fucus* was a better predictor of growth and mortality than age. Since I could not age the *Fucus* transplants in this study, I randomly chose reproductively mature individuals, so that I did not skew the size distribution by the inclusion of juveniles.

Ecological factors such as competition for space and grazing can influence the sizes and morphologies of plants which are present during

different times of the year. Schiel and Choat (1980), Cousens and Hutchings (1983), Reed (1990a) and Martinez and Santelices (1992) present evidence that sizes of seaweeds may be affected by density-dependent intra- and inter-specific competition. Transplants in this study were all approximately uniformly spaced and I have no evidence that sizes of transplants may have been affected by competition.

Certain annual or ephemeral algae of the mid to high intertidal zones have heteromorphic life histories and exist as upright morphs during the summer and as crustose or boring morphs during other times of the year. The selection and continued maintenance of these different morphologies have been shown to be a function of the spatial and temporal variations in grazing (Lubchenco and Cubit 1980, Dethier 1981).

The levels of grazing and physical stress may also influence the morphology of an algal thallus within a particular life history phase. Hay (1981) has shown that algae growing in physically stressful or moderately grazed habitats tend to grow as turfs rather than spatially separated individuals. The activities of grazers can determine the points at which a plant breaks (Santelices et al. 1980). Black (1976) showed that damage by the limpet *Acmaea insessa* pruned the blades of *Egregia,* making it as a whole, less susceptible to removal by waves.

The most common grazers at Fogarty Creek Point were the limpet *Lottia digitalis* at the wave-exposed site and the snails *Tegula funebralis* and *Littorina scutulata* at the wave-protected site. Although these grazers are relatively abundant at both sites, they probably have little effect on adult *Fucus* plants but may graze heavily on young *Fucus* and other algae. Lubchenco (1983) found that *Littorina littorea* in New England harm

young *Fucus*, and may actually benefit older *Fucus* by grazing epiphytes. I have observed *Littorina* and limpets grazing epiphytes on *Fucus*, but never grazing the adult *Fucus*. The limpets may actually have a larger effect on the mortality of the *Fucus* by bulldozing holdfasts than on the sizes of the plants by consumption.

VanAlstyne (1988) showed that *Fucus distichus* (now known as *Fucus gardneri*) possesses inducible chemical defenses against herbivory. Concentrations of these chemicals are highest at the site of injury and may be induced by herbivore grazing or mechanical damage. Production of adventitious branches could be induced by mechanical damage or herbivore grazing (VanAlstyne 1989). VanAlstyne (unpublished data) found that naturally occurring wave-exposed *Fucus* had higher levels of phenolic compounds than wave-protected plants. This may be due to the fact that wave-exposed plants suffer more mechanical damage due to wave pruning than do wave-protected plants.

The plastic aquarium plants provide additional evidence that wave forces alone can exert a strong influence on size. Plastic plants are not affected by herbivory, competition, nutrient or light levels. The abrupt reduction in size of the plastic plants at the wave-exposed site relative to the protected site provides evidence that wave forces may be the primary mechanism responsible for the observed pattern of decreasing plant sizes with increasing wave exposure.

CONCLUSIONS

Results of the models of predicted optimal sizes fall very close to the mean sizes of plants observed in the field, suggesting that hydrodynamic forces have a large influence on the sizes to which *Fucus* plants can grow. Plants seem to be able to grow as large as the environment will allow while maintaining a relatively high probability of survival. The transplant experiment provides empirical support for the idea that wave forces can set mechanical limits to size in *Fucus* and that wave exposure has a direct influence on plant size, but not on survival. With further developments of models to describe the relationships between wave forces and sizes of organisms, field experiments to test these models and ways to predict onshore wave forces based on offshore buoy information, we can make significant contributions to understanding and predicting how the structure of wave-swept intertidal communities may be influenced by the physical stress of wave forces and how these communities may change in the face of potential changes in global weather patterns.

TABLES

Table II.1.

Breaking force (N) as a function of plant area (A) (m^2):

$$Force = x + y\,A^z$$

Sampling date	x	y	z	r^2	p value
March 1992	-16.430	68.492	0.134	0.197	<<0.001
August 1992	-1.657	96.871	0.276	0.235	<<0.001
February 1993	-4.279	183.799	0.318	0.482	<<0.001

Table II.2.

Modified Weibull distribution for the probability, P that a given relative breaking force is less than a value f':

$$P(f') = \exp - \{[a-bf')/(a-be)]^{1/b}\}$$

Sampling date	a	b	e	r^2	p value
March 1992	0.269	-0.351	0.636	0.820	<<0.001
August 1992	0.410	-0.089	0.717	0.932	<<0.001
February 1993	0.554	0.270	0.829	0.949	<<0.001

Table II.3.

Constants in the allometric function:

$$V = f\,A^g$$

Sampling date	f	g	r^2	p value
March 1992	0.002	1.079	0.925	<<0.001
August 1992	0.040	1.584	0.933	<<0.001
February 1993	0.002	1.024	0.878	<<0.001

Table II.4.

Two-way analysis of variance (ANOVA) of the effect of time of year (date) and wave exposure (exposure) on *Fucus* areas, lengths, weights and breaking strengths sampled from wave-exposed and wave-protected sites at Fogarty Creek Point (FCP) in March 1992, August 1992 and February 1993. Date and exposure were considered fixed and sums of squares are type III.

	df	MS	F-Ratio	p
AREA				
Date	2	0.00018	24.994	<0.0001
Exposure	1	0.00326	441.752	<0.0001
Date x Exposure	2	0.00010	13.362	<0.0001
Error	594	0.00001		
LENGTH				
Date	2	0.06031	84.707	<0.0001
Exposure	1	0.79031	1110.102	<0.0001
Date x Exposure	2	0.04932	69.274	<0.0001
Error	594	0.00071		
WEIGHT				
Date	2	0.00331	37.083	<0.0001
Exposure	1	0.01284	143.794	<0.0001
Date x Exposure	2	0.00201	22.550	<0.0001
Error	594	0.00009		
STRENGTH				
Date	2	29.480	18.235	<0.0001
Exposure	1	48.631	30.081	<0.0001
Date x Exposure	2	2.898	1.793	0.1675
Error	587	1.627		

Table II.5.

Predicted optimal sizes (optimal) and mean observed sizes (mean) of *Fucus* at both wave-exposed (E) and wave-protected (P) sites at FCP in March 1992, August 1992, and February 1993.

Date	Exposure	Accel. (m/s^2)	Optimal (m^2)	Mean (m^2)
MARCH	P	200 - 300	0.0047 - 0.0034	0.0040
MARCH	E	600 - 700	0.0011 - 0.0008	0.0010
AUGUST	P	100 - 200	0.0070 - 0.0045	0.0073
AUGUST	E	500 - 600	0.0017 - 0.0015	0.0016
FEBRUARY	P	200 - 300	0.0078 - 0.0050	0.0062
FEBRUARY	E	600 - 700	0.0013 - 0.0011	0.0009

Table II.6.

Comparison of proportional survival and expected mortality of plants in (**a**) the protected to exposed treatment (P to E) versus the protected controls (P to P); (**b**) the exposed to protected treatment (E to P) versus the exposed controls (E to E); (**c**) the protected to protected controls (P to P) versus the protected tagged plants (P); and (**d**) the exposed to exposed controls (E to E) versus the exposed tagged plants (E). Short term logrank statistics (LR) between consecutive census dates are shown. d_{1i} = number of deaths in group 1 at time interval i. d_{2i} = number of deaths in group 2 at time interval i. E_{1i} = expected number of deaths in group 1 in interval i. E_{2i} = expected number of deaths in group 2 in interval i. LR = Logrank statistic comparing mortality risks between the treatment and control in time interval i and over the entire year.

$$LR = [(d_1 - E_1)^2/E_1 + (d_2 - E_2)^2/E_2]$$

Logrank statistic is compared to a chi-squared distribution.
** = $p < 0.01$; * = $p < 0.05$; NS = not significant.

a)

i	d_{1i}	d_{2i}	E_1	E_{2i}	LR	p
1	18	1	9.822	9.178	14.100	**
2	6	11	7.384	9.616	0.485	NS
3	10	12	9.927	12.07	0.001	NS
4	2	4	2.700	3.300	0.330	NS
5	3	4	3.241	3.759	0.033	NS
6	5	8	6.085	6.915	0.364	NS
7	2	3	2.500	2.500	0.200	NS
8	3	3	3.103	2.897	0.007	NS
9	3	3	3.130	2.870	0.011	NS
10	2	1	1.588	1.412	0.227	NS
11	6	4	5.000	5.000	0.400	NS
12	0	1	0.250	0.750	0.333	NS
year	60	55	54.73	60.27	0.968	NS

Table II.6 (Continued)

b)

i	$d1i$	$d2i$	$E1$	$E2i$	LR	p
1	4	10	6.881	7.119	2.373	NS
2	15	5	10.380	9.615	4.267	*
3	6	10	7.429	8.571	0.513	NS
4	5	5	4.853	5.147	0.009	NS
5	2	4	2.897	3.103	0.537	NS
6	6	7	6.500	6.500	0.077	NS
7	0	1	0.513	0.487	1.053	NS
8	1	2	1.579	1.421	0.448	NS
9	5	1	3.257	2.743	2.040	NS
10	4	2	2.897	3.103	0.813	NS
11	2	7	3.913	5.087	1.655	NS
12	3	2	2.857	2.143	0.017	NS
year	53	56	53.960	55.040	0.034	NS

c)

i	$d1i$	$d2i$	$E1$	$E2i$	LR	p
1	1	8	4.500	4.500	5.444	*
2	11	5	8.533	7.467	1.528	NS
3	12	5	8.596	8.404	2.728	NS
4	4	3	3.208	3.792	0.361	NS
5	4	4	3.569	4.431	0.094	NS
6	8	3	4.825	6.175	3.723	NS
7	3	6	3.326	5.674	0.051	NS
8	3	9	4.541	7.459	0.841	NS
9	3	1	1.760	2.240	1.560	NS
10	1	5	2.286	3.714	1.168	NS
11	4	3	3.267	3.733	0.309	NS
year	54	52	48.410	57.590	1.188	NS

d)

i	$d1i$	$d2i$	$E1$	$E2i$	LR	p
1	10	9	9.421	9.579	0.070	NS
2	34	40	36.270	37.730	0.280	NS
3	1	1	1.143	0.857	0.042	NS
4	2	2	2.308	1.692	0.097	NS
5	7	1	4.727	3.273	2.671	NS
year	54	53	53.870	53.130	0.001	NS

Table II.7.

Repeated measures ANOVA of the effect of transplant site (treatment) and date on mean planform areas of plants, comparing P to E with P to P (Protected) and E to P with E to E (Exposed).

PROTECTED

	df	MS	F-Ratio	p
Between Subjects				
Treatment	1	19.279	14.307	0.002
Error	12	1.347		
Within Subjects				
Date	8	2.333	8.131	<0.001
Treatment x Date	8	3.367	11.737	<0.001
Error	96	0.286		

Multivariate Repeated Measures Analysis (df = 8, 5)

	Wilks' Lamba	F-Ratio	p
Date	0.062	9.529	0.011
Treatment x Date	0.067	8.633	0.014

EXPOSED

	df	MS	F-Ratio	p
Between Subjects				
Treatment	1	29.943	16.721	<0.001
Error	19	1.791		
Within Subjects				
Date	8	1.027	2.530	0.013
Treatment x Date	8	2.232	5.490	<0.001
Error	152	0.406		

Multivariate Repeated Measures Analysis (df = 8, 12)

	Wilks' Lamba	F-Ratio	p
Date	0.294	3.615	0.022
Treatment x Date	0.333	3.000	0.042

Table II.8.

Repeated measures ANOVA of the effect of transplant site (treatment) and date on mean length of plants, comparing P to E with P to P (Protected) and E to P with E to E (Exposed).

PROTECTED

	df	MS	F-Ratio	p
Between Subjects				
Treatment	1	2.499	4.874	0.047
Error	12	0.513		
Within Subjects				
Date	10	0.146	1.781	0.071
Treatment x Date	10	0.531	6.463	<0.001
Error	120	0.082		

Multivariate Repeated Measures Analysis (df = 10, 3)

	Wilks' Lamba	F-Ratio	p
Date	0.040	7.150	0.066
Treatment x Date	0.004	63.933	0.002

EXPOSED

	df	MS	F-Ratio	p
Between Subjects				
Treatment	1	1.439	3.058	0.095
Error	21	0.471		
Within Subjects				
Date	10	0.160	3.123	<0.001
Treatment x Date	10	0.173	3.377	<0.001
Error	210	0.051		

Multivariate Repeated Measures Analysis (df = 10, 12)

	Wilks' Lamba	F-Ratio	p
Date	0.218	4.285	0.010
Treatment x Date	0.294	2.878	0.043

Table II.9.

Two-way ANOVA of the effect of transplant site (treatment) and time of year (season) on maximum planform areas of plants, comparing P to E with P to P (Protected) and E to P with E to E (Exposed). Treatment and season were considered fixed and sums of squares are type III.

	df	MS	F-Ratio	p
PROTECTED				
Treatment	1	384.800	172.621	<0.001
Season	3	42.189	18.926	<0.001
Treatment x Season	3	32.488	14.556	<0.001
Error	16	2.229		
EXPOSED				
Treatment	1	29.260	99.328	<0.001
Season	3	0.810	2.751	0.077
Treatment x Season	3	1.495	5.074	0.012
Error	16	0.295		

Table II.10.

Two-way ANOVA of the effect of transplant site (treatment) and time of year (season) on maximum lengths of plants, comparing P to E with P to P (Protected) and E to P with E to E (Exposed). Treatment and season were considered fixed and sums of squares are type III.

	df	MS	F-Ratio	p
PROTECTED				
Treatment	1	0.861	45.561	<0.001
Season	3	0.177	9.397	<0.001
Treatment x Season	3	0.149	7.894	0.001
Error	18	0.019		
EXPOSED				
Treatment	1	0.409	49.193	<0.000
Season	3	0.003	0.381	0.768
Treatment x Season	3	0.042	5.063	0.010
Error	18	0.008		

Table II.11.

Repeated measures ANOVA of the effect of transplant site (treatment) and date on mean length of plants, comparing areas P to P with areas of protected tagged plants (Protected) and areas of E to E with areas of exposed tagged plants (Exposed).

PROTECTED

	df	MS	F-Ratio	p
Between Subjects				
Treatment	1	0.402	0.548	0.468
Error	18	0.734		
Within Subjects				
Date	9	0.717	29.555	<0.001
Treatment x Date	10	0.013	0.557	0.831
Error	162	0.024		

Multivariate Repeated Measures Analysis (df = 9, 10)

	Wilks' Lamba	F-Ratio	p
Date	0.015	71.119	0.000
Treatment x Date	0.326	2.302	0.105

EXPOSED

	df	MS	F-Ratio	p
Between Subjects				
Treatment	1	0.304	1.274	0.271
Error	22	0.239		
Within Subjects				
Date	3	0.143	2.168	0.098
Treatment x Date	3	0.147	2.249	0.091
Error	66	0.065		

Multivariate Repeated Measures Analysis (df = 3, 20)

	Wilks' Lamba	F-Ratio	p
Date	0.442	8.412	<0.001
Treatment x Date	0.764	2.058	0.138

Table II.12.

Two-way ANOVA of the effect of transplant site (treatment) and time of year (season) on maximum lengths of plants, comparing P to P with protected tagged plants (Protected) and E to E with exposed tagged plants (Exposed). Treatment and season were considered fixed and sums of squares are type III.

	df	MS	F-Ratio	p
PROTECTED				
Treatment	1	0.0001	0.123	0.913
Season	3	0.0290	3.145	0.054
Treatment x Season	3	0.0013	0.140	0.934
Error	16	0.0092		
EXPOSED				
Treatment	1	0.6021	2.588	0.146
Season	1	3.3750	14.516	0.005
Treatment x Season	1	0.0420	0.179	0.683
Error	8	0.2330		

Table II.13.

Two-way ANOVA of the effect of transplant site (treatment) and date on number of repoductive blades per thallus, comparing P to E with P to P (Protected) and E to P with E to E (Exposed). Treatment and date were considered fixed and sums of squares are type III.

	df	MS	F-Ratio	p
PROTECTED				
Treatment	1	17.005	59.106	<0.001
Date	10	0.326	1.133	0.336
Treatment x Date	10	0.735	2.556	0.005
Error	373	0.288		
EXPOSED				
Treatment	1	9.610	31.947	<0.001
Date	10	1.659	5.514	<0.001
Treatment x Date	10	1.263	4.199	<0.001
Error	436	0.301		

Table II.14.

Number of branches remaining on plastic aquarium plants at exposed and protected sites from March 31, 1994 to June 23, 1994.

	# BRANCHES REMAINING					
	March 31	April 2	April 4	April 28	May 25	June 23
PROTECTED	7	7	7	7	7	6
PROTECTED	7	7	7	7	7	1
PROTECTED	7	5	5	5	5	5
EXPOSED	7	1	0	0	0	0
EXPOSED	7	5	0	0	0	0
EXPOSED	7	4	0	0	0	0

FIGURES

Figure II.1. A view of Fogarty Creek Point, OR facing west. The arrow marked "E" shows the location of the wave-exposed site, and the arrow marked "P" shows the location of the wave-protected site.

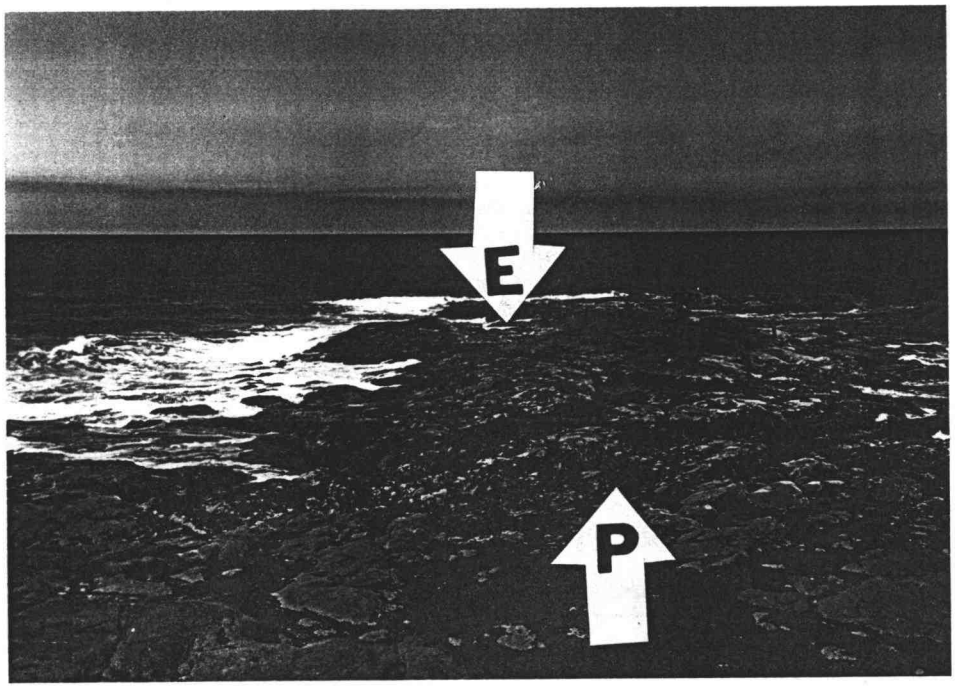
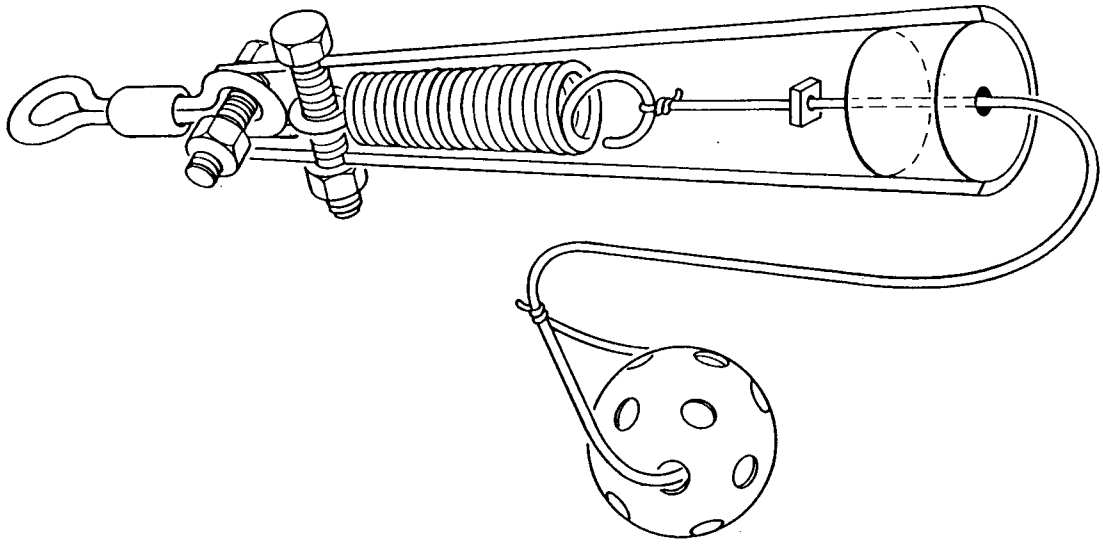


Figure II.2. Maximum wave force meter. (a) Cut-away view: shows the attachment of the stainless steel spring to both the nylon bolt and braided dacron line. (b) Complete view: shows the attachment of the device to the stainless steel quick link, and the quick link attachment to the stainless steel eyebolt, which is screwed into the rock and surrounded with marine epoxy putty.

A



B

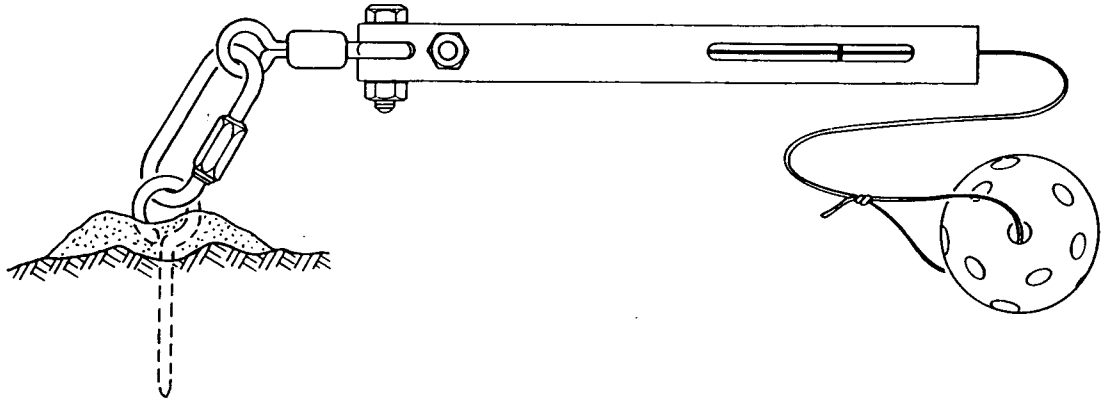


Figure II.3. Representative*Fucus gardneri* specimens collected from the wave-protected area (P) and the wave-exposed area (E).

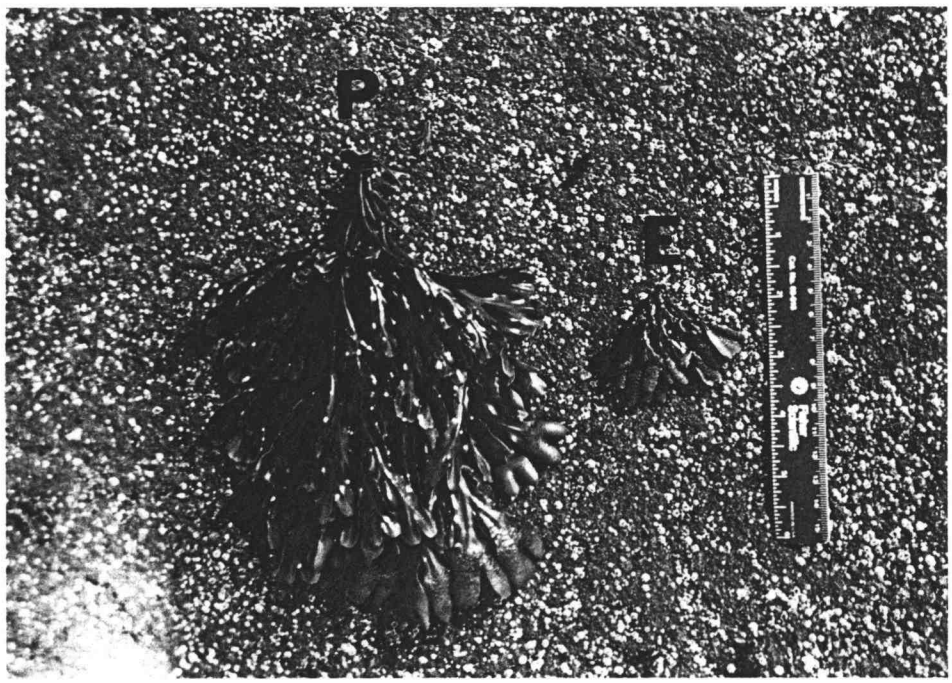


Figure II.4. A typical wave-protected *Fucus* transplant showing the marine epoxy/rock adhesion and numbered plastic label.

Figure II.5. Mean sizes of *Fucus gardneri* at Fogarty Creek Point, OR at wave exposed (solid bars) and wave-protected (stippled bars) sites ± 1 s.e.m. in March 1992, August 1992 and February 1993. At all sites n=100 plants. (a) Planform area refers to the area of the plant projected to flow, (b) Length is the length from the holdfast to the tip of the longest branch, and (c) Weight is the wet weight of the plant after shaking and removing surface water with a paper towel.

Figure II.5

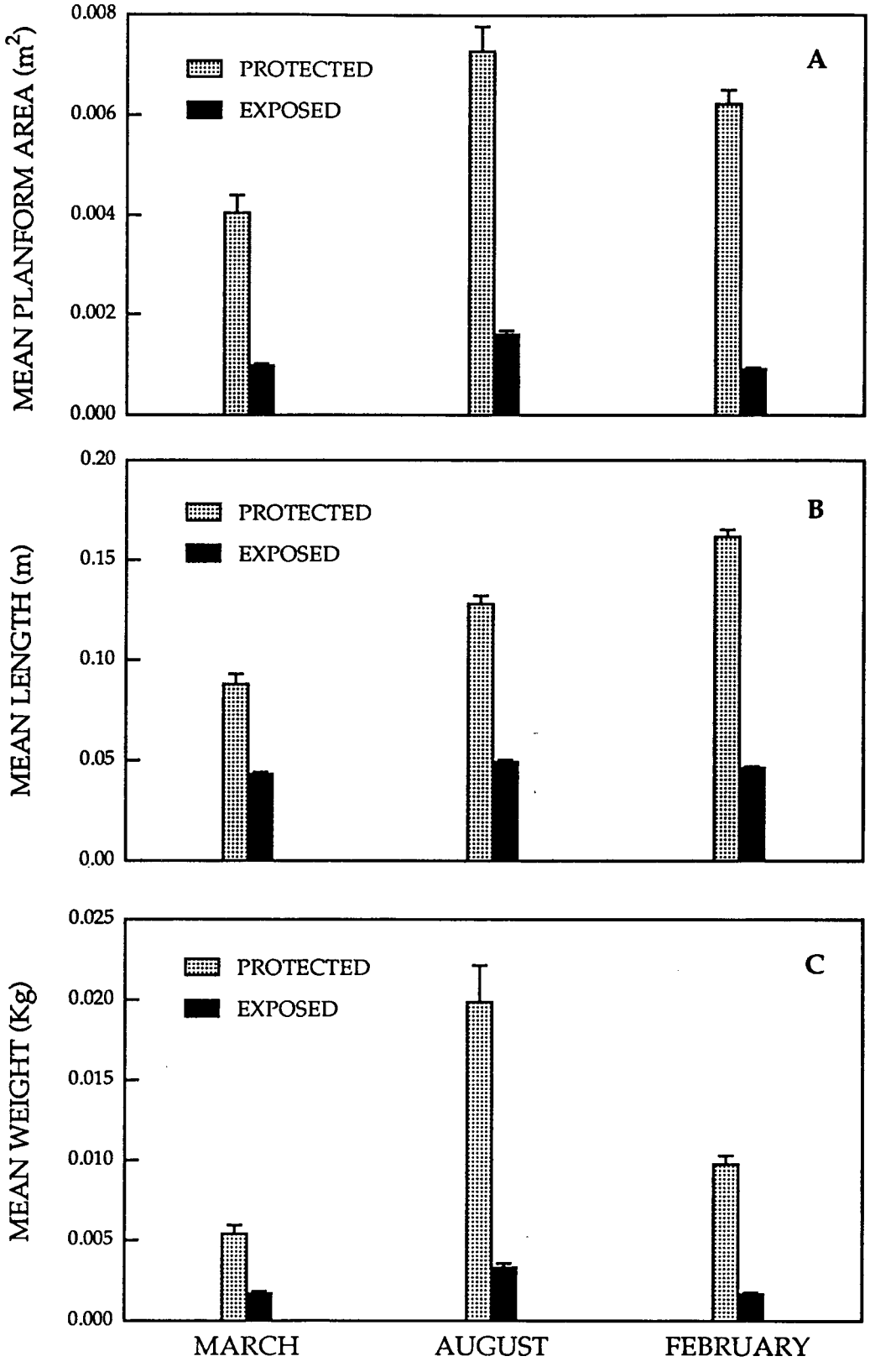

MEAN PLANFORM AREA (m^2)
0.008
0.006
0.004
0.002
0.000
PROTECTED
EXPOSED
A
MEAN LENGTH (m)
0.20
0.15
0.10
0.05
0.00
PROTECTED
EXPOSED
B
MEAN WEIGHT (Kg)
0.025
0.020
0.015
0.010
0.005
0.000
PROTECTED
EXPOSED
C
MARCH
AUGUST
FEBRUARY

Figure II.6. Mean breaking strengths of *Fucus gardneri* at Fogarty Creek Point, OR at wave exposed (solid bars) and wave-protected (stippled bars) sites ± 1 s.e.m. in March 1992, August 1992 and February 1993. At all sites n=100 plants. Breaking strength is equal to the amount of force required to break or dislodge a plant divided by the cross sectional area of the break.

Figure II.6

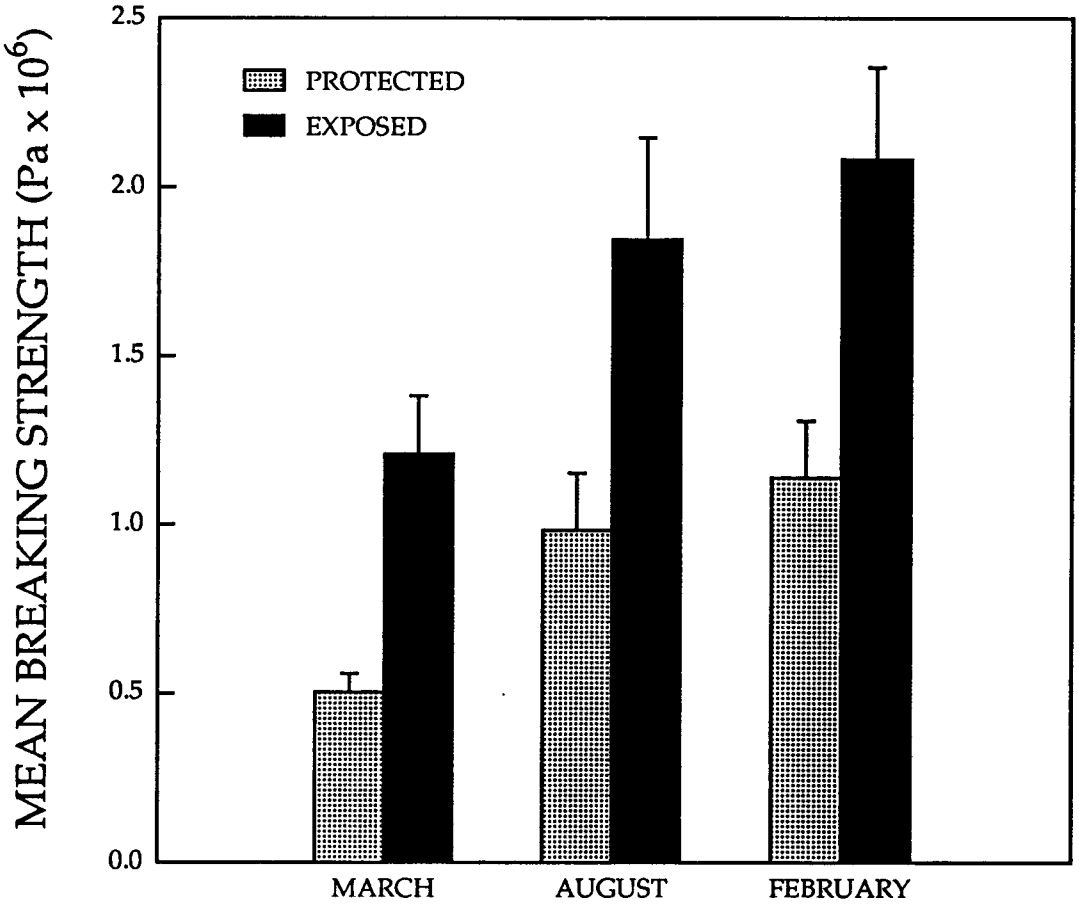

MEAN BREAKING STRENGTH (Pa x 10^6)
2.5
2.0
1.5
1.0
0.5
0.0
PROTECTED
EXPOSED
MARCH
AUGUST
FEBRUARY

Figure II.7. The probability that a *Fucus* plant of a given size (planform area) will survive a three month period at either a wave-exposed site where Hm=2 m or a wave-protected site where Hm=1 m, given several levels of acceleration (100-300 m/s^2 for the wave-protected site and 500-700 m/s^2 for the wave-exposed site). *Fucus* sampled in winter (February and March) are more likely to experience higher accelerations than those sampled in summer (August). The mean observed sizes of *Fucus* at each site for each date are indicated on the abcissa as E = mean observed size of wave-exposed plants, P = mean observed size of wave-protected plants. (Note different scales on the abcissa for protected versus exposed data).

Figure II.7

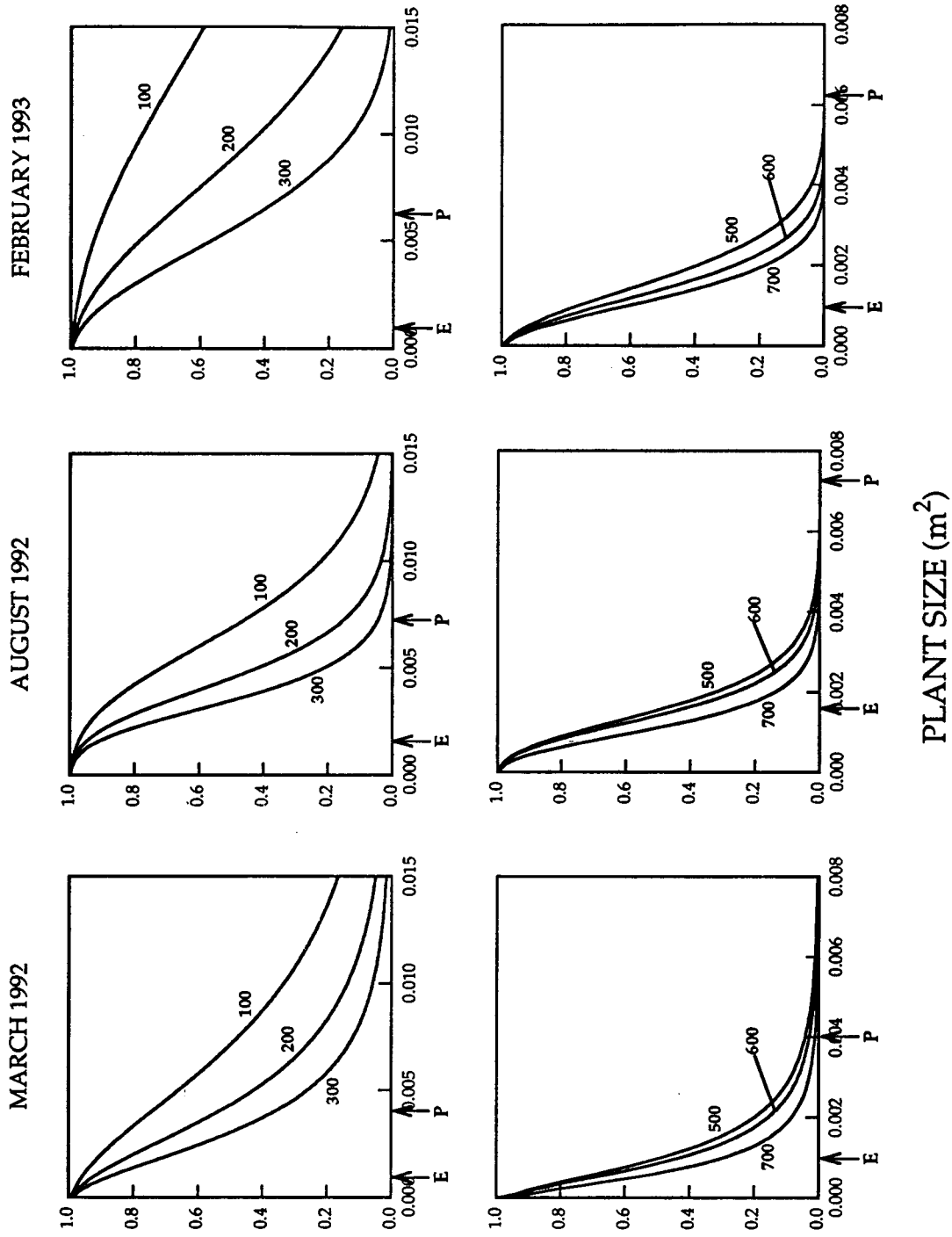

MARCH 1992
AUGUST 1992
FEBRUARY 1993
WAVE-PROTECTED AREA
WAVE-EXPOSED AREA
PROBABILITY OF SURVIVAL
PLANT SIZE (m²)
100
200
300
500
600
700
E
P

Figure II.8. Index of reproductive output for *Fucus* plants of various sizes (planform area) for a three month period at either a wave-exposed site where Hm=2 m or a wave-protected site where Hm=1 m given several levels of acceleration (100-300 m/s^2 for the wave-protected site and 500-700 m/s^2 for the wave-exposed site). The mean observed sizes of *Fucus* at each site for each date are indicated on the abcissa as E = mean observed size of wave-exposed plants, P = mean observed size of wave-protected plants. Predicted optimal plant areas are near the mean sizes observed in the winter months (March and February) when acclerations are between 600-700 m/s^2 at the wave-exposed site and when accelerations are between 200-300 m/s^2 at the wave-protected site. Predicted optimal plant areas are near the mean sizes observed in August when accelerations are between 500-600 m/s^2 at the wave-exposed site and when accelerations are between 100-200 m/s^2 at the wave-protected site.

Figure II.8

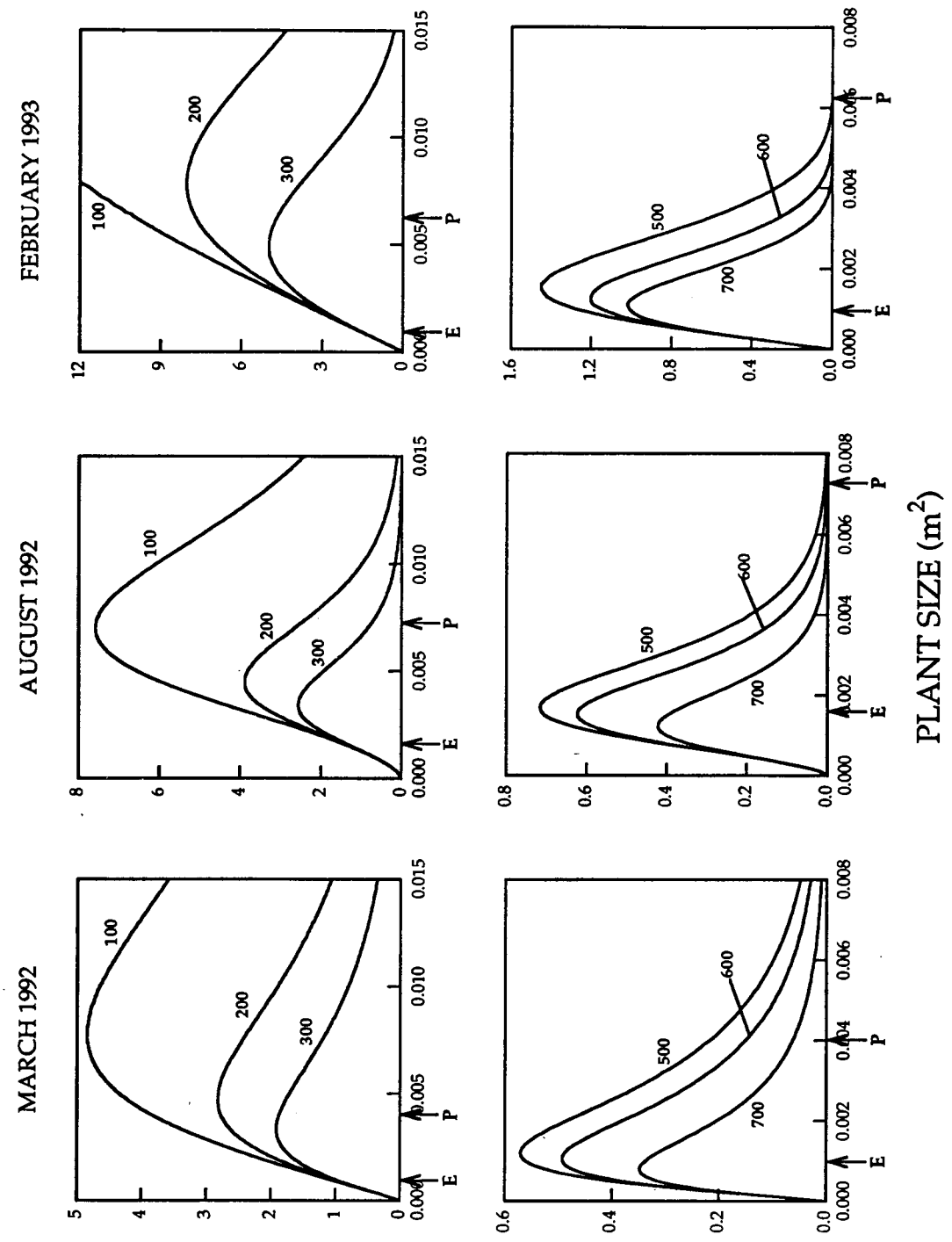

MARCH 1992
AUGUST 1992
FEBRUARY 1993
WAVE-PROTECTED AREA
WAVE-EXPOSED AREA
INDEX OF REPRODUCTIVE OUTPUT (cm³)
PLANT SIZE (m²)
E
P
100
200
300
500
600
700

Figure II.9. Bars represent mean maximum wave forces (N) recorded at Fogarty Creek Point, OR at both wave-exposed (solid bars) and protected (stippled bars) sites ± 1 s.e.m. For most dates n= 5 - 8 wave meters. Diamonds represent maximum wave forces predicted for FCP wave-exposed areas based on data from buoy #50 (145 km offshore from FCP) (see text for details).

Figure II.9

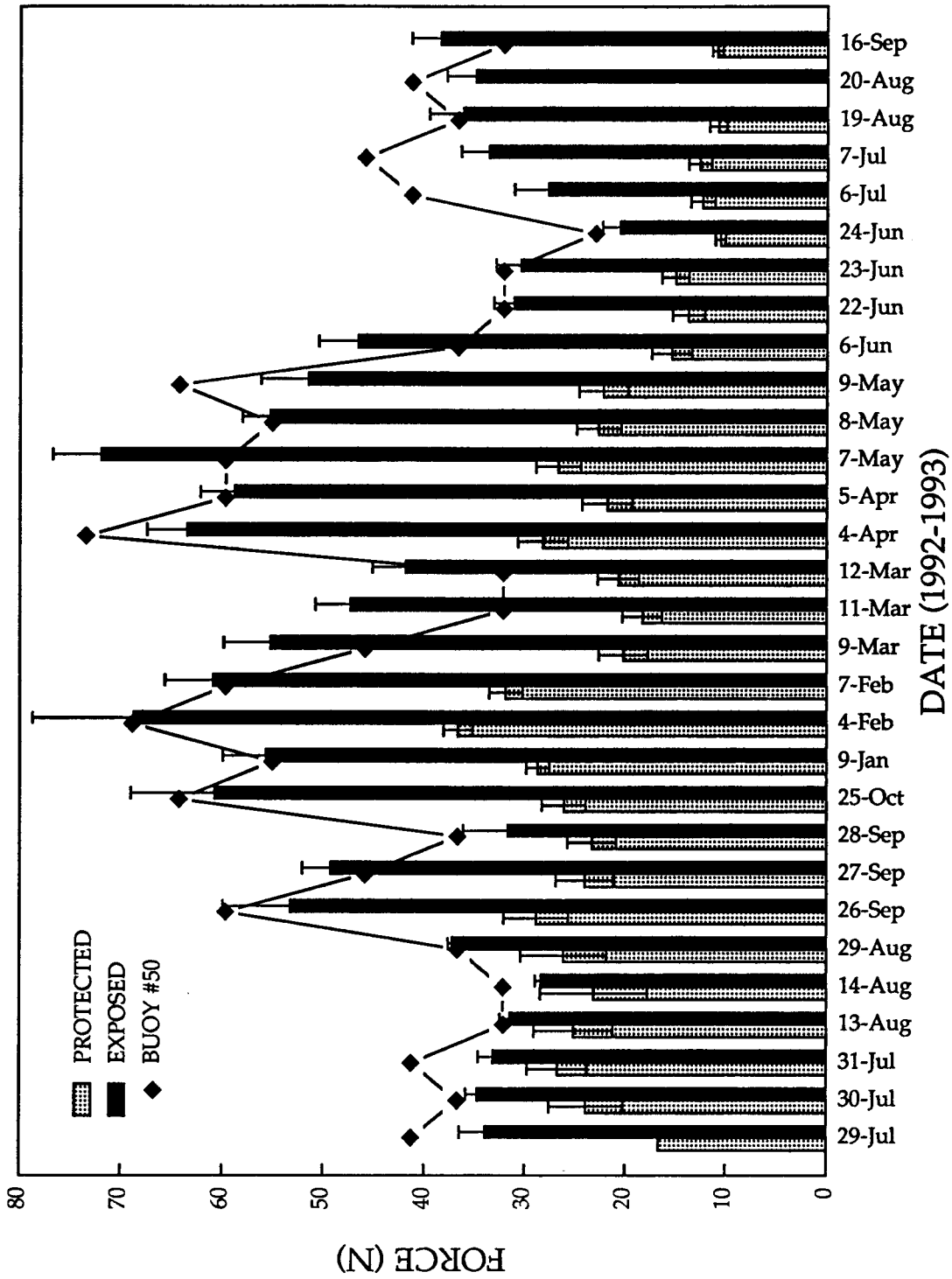

PROTECTED
EXPOSED
BUOY #50
80
70
60
50
40
30
20
10
0
FORCE (N)
16-Sep
20-Aug
19-Aug
7-Jul
6-Jul
24-Jun
23-Jun
22-Jun
6-Jun
9-May
8-May
7-May
5-Apr
4-Apr
12-Mar
11-Mar
9-Mar
7-Feb
4-Feb
9-Jan
25-Oct
28-Sep
27-Sep
26-Sep
29-Aug
14-Aug
13-Aug
31-Jul
30-Jul
29-Jul
DATE (1992-1993)

Figure II.10. Mean and maximum significant wave heights recorded by the NOAA Data Buoy Center from buoy #46040 (44.8° N, 124.3° W). Wave observations are taken each hour during a 20 minute averaging period with a sample taken every 0.67 seconds. (a) Mean significant wave height is the average height of the highest 1/3 of waves during the averaging period each hour. (b) Maximum significant wave height is the highest value recorded each month.

Figure II.10

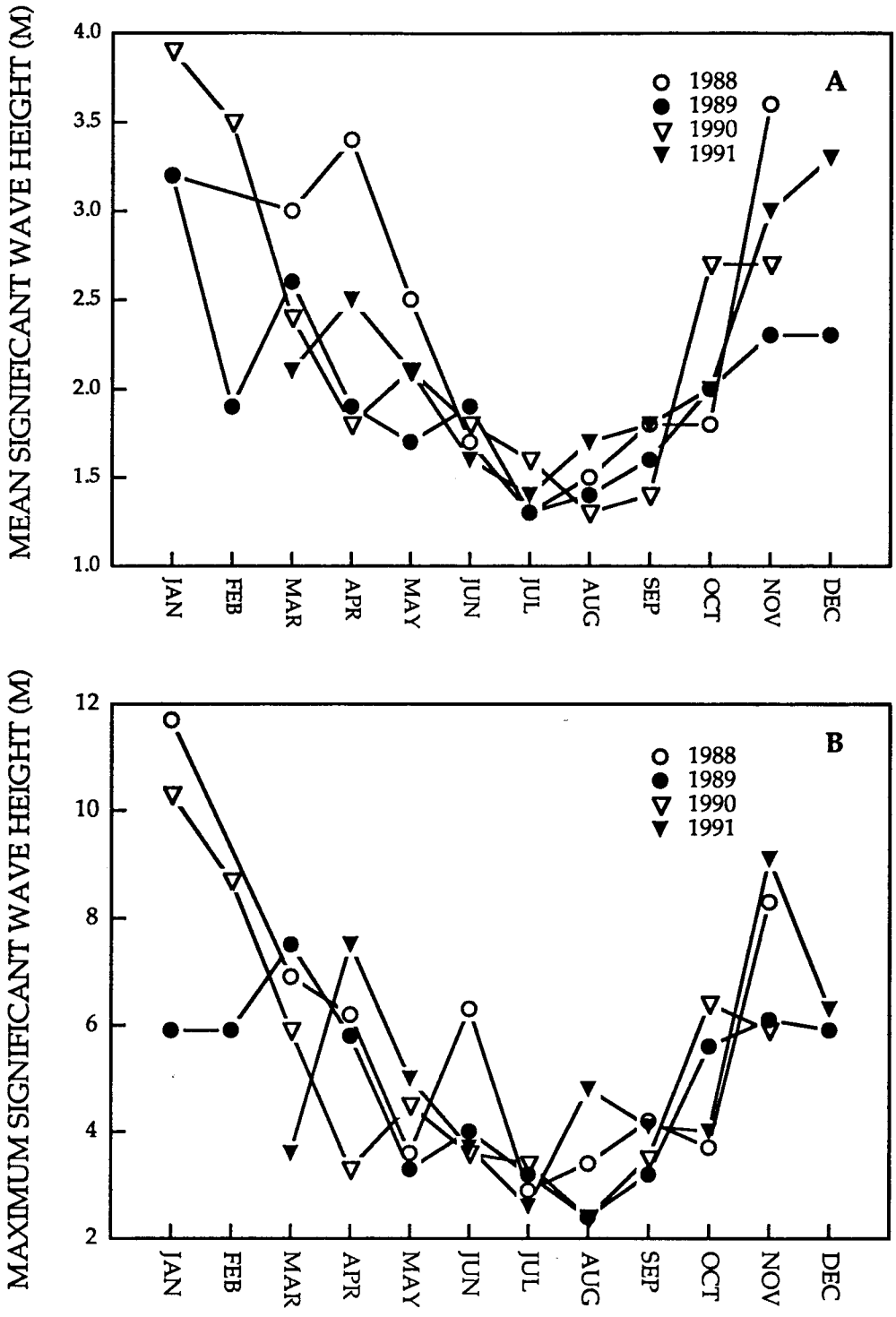

MEAN SIGNIFICANT WAVE HEIGHT (M)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
1988
1989
1990
1991
A
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
MAXIMUM SIGNIFICANT WAVE HEIGHT (M)
12
10
8
6
4
2
1988
1989
1990
1991
B
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure II.11. Correlation between mean measured maximum wave force at the FCP wave-exposed site (recorded from the maximum wave force meters) and predicted maximum wave force using the maximum value for wave height from buoy #50 over the 24 hour period that the maximum wave force meter was deployed.

Figure II.11

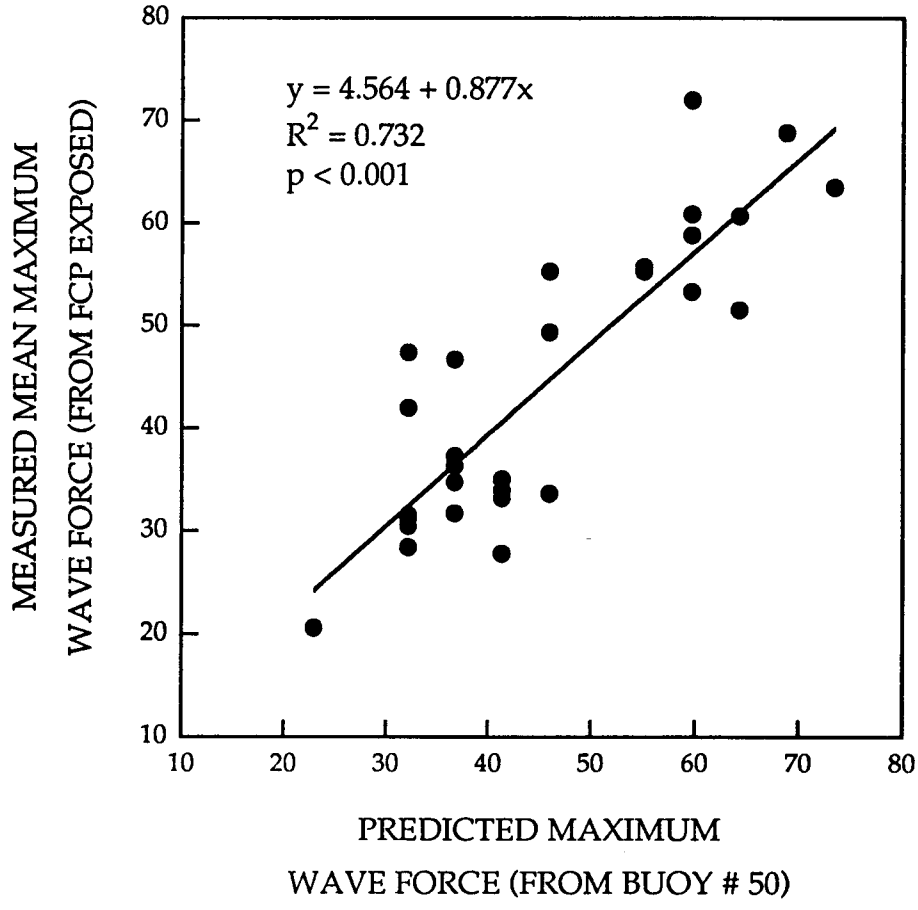

y = 4.564 + 0.877x
R^2 = 0.732
p < 0.001
MEASURED MEAN MAXIMUM
WAVE FORCE (FROM FCP EXPOSED)
PREDICTED MAXIMUM
WAVE FORCE (FROM BUOY # 50)
10
20
30
40
50
60
70
80

Figure II.12. Predicted monthly mean and maximum wave forces at FCP wave-exposed site for 1988, 1989, 1990 and 1991 based on monthly mean and maximum significant wave heights from buoy #46040 (60 km offshore from FCP) using equation 7.

Figure II.12

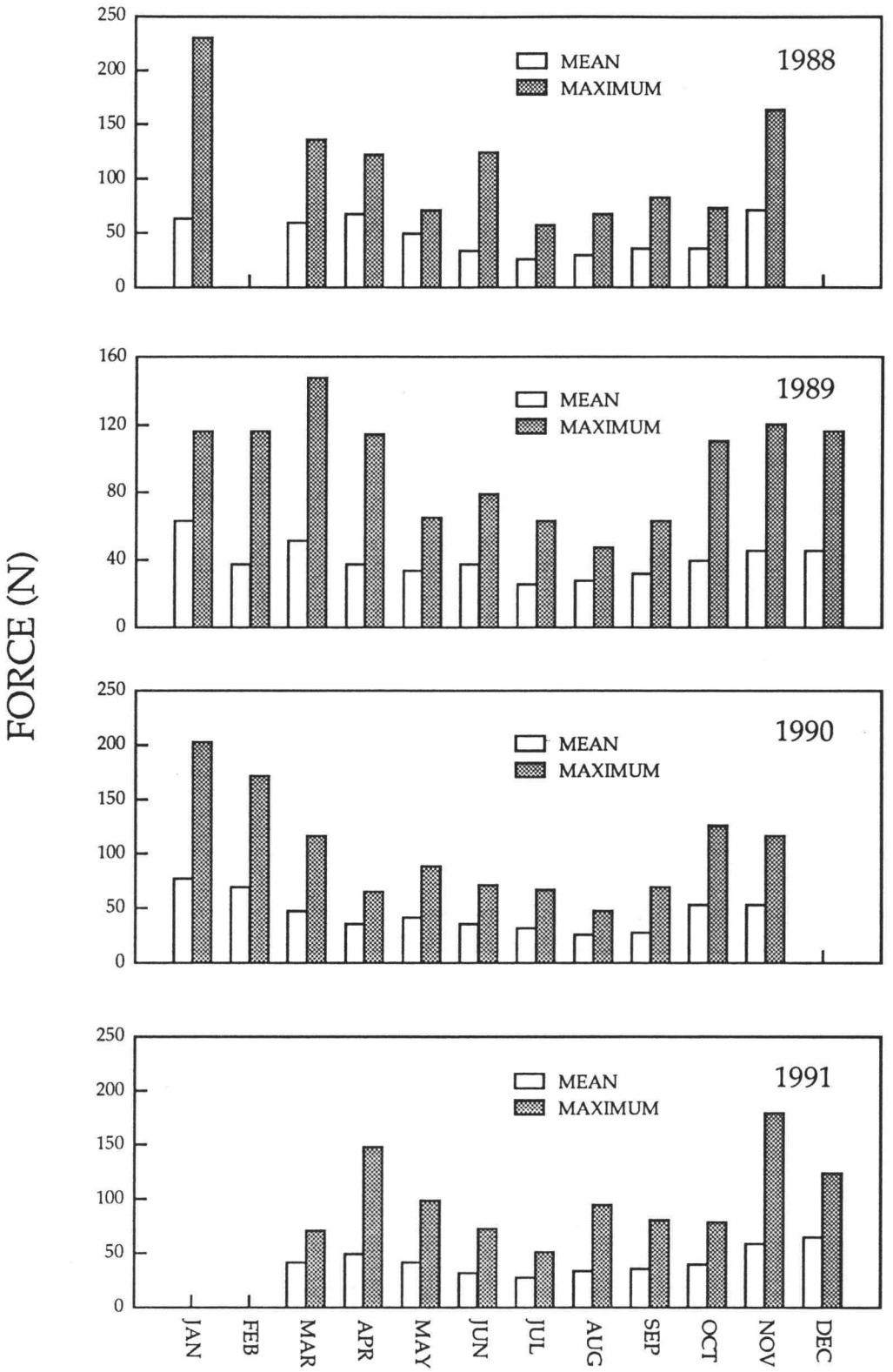

FORCE (N)
MEAN
MAXIMUM
1988
1989
1990
1991
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure II.13. Percentage of treatment and control transplants surviving over the course of the experiment. Circles refer to plants from the wave-protected site and triangles refer to plants from the wave-exposed site. Treatment transplants are represented as open symbols, and controls as solid symbols. Percent survival did not differ between either the protected or the exposed treatment transplants and controls over the duration of the experiment.

Figure II.13

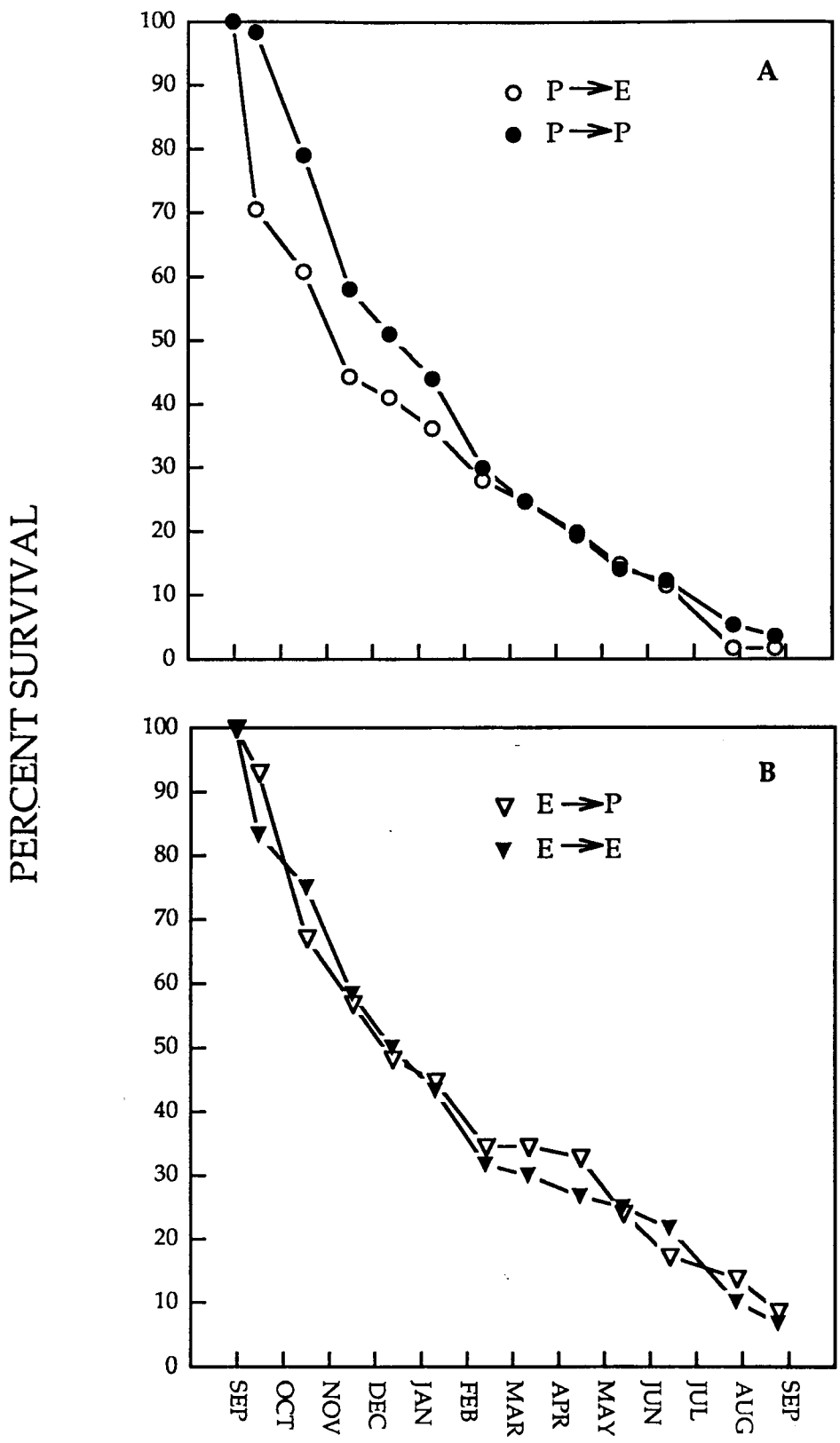

PERCENT SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
A
P→E
P→P
B
E→P
E→E
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Figure II.14. Percentage of control transplants and tagged plants surviving over the course of the experiment. Squares refer to plants from the wave-protected site and diamonds refer to plants from the wave-exposed site. Control transplants are represented as solid symbols, and tagged plants as open symbools. Percent survival did not differ between either the protected or the exposed control transplants and tagged plants over the experiment.

Figure II.14

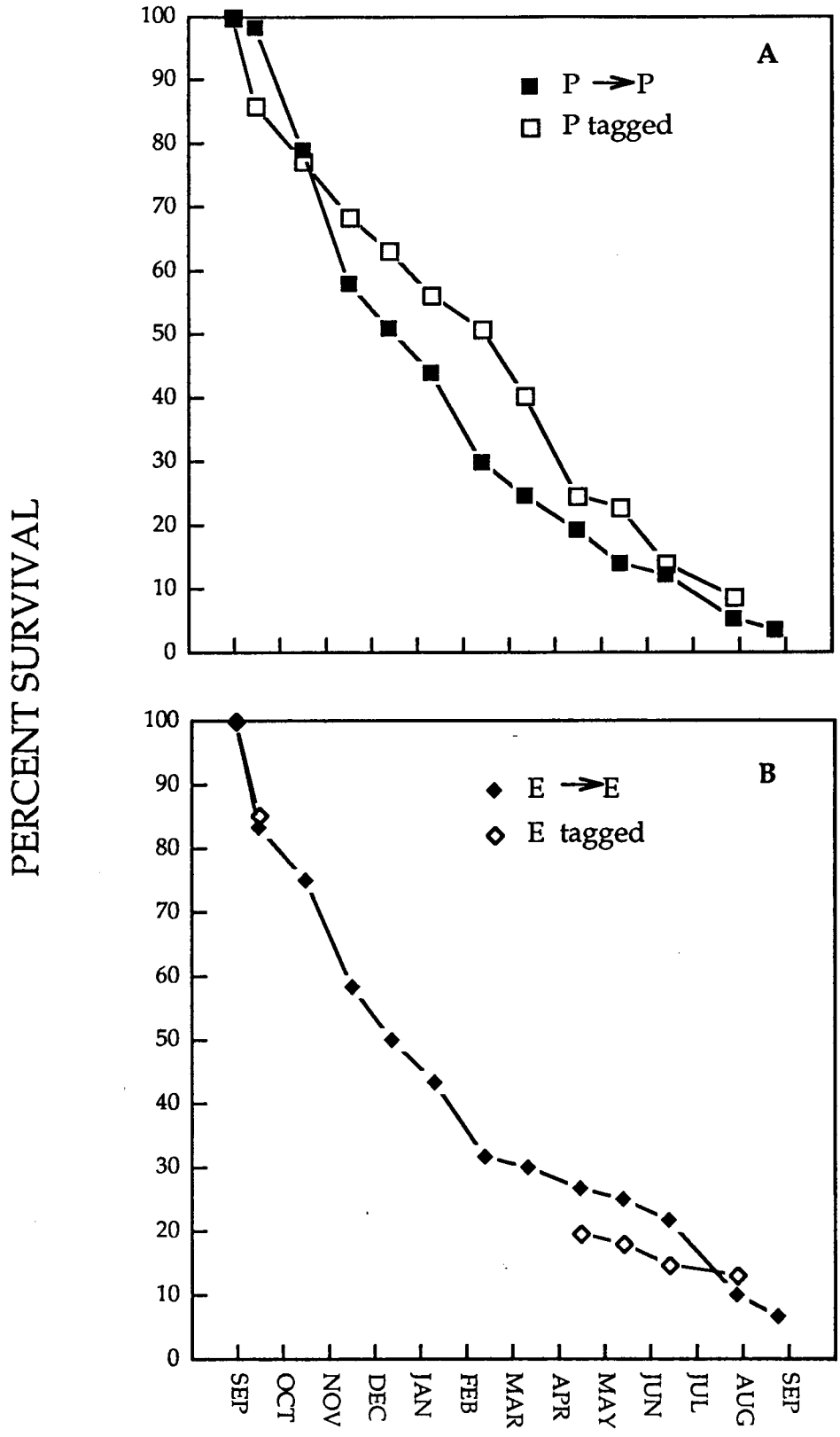

PERCENT SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
A
P →P
P tagged
B
E →E
E tagged
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Figure II.15. Mean areas of plants remaining in each treatment and control group over time ± 1 s.e.m. Treatment transplants are represented as open symbols and controls as closed symbols. In P to E starting n=60, final n=1. In P to P starting n=60, final n=2. In E to P starting n=60, final n=5. In E to E starting n=60, final n=3.

Figure II.15

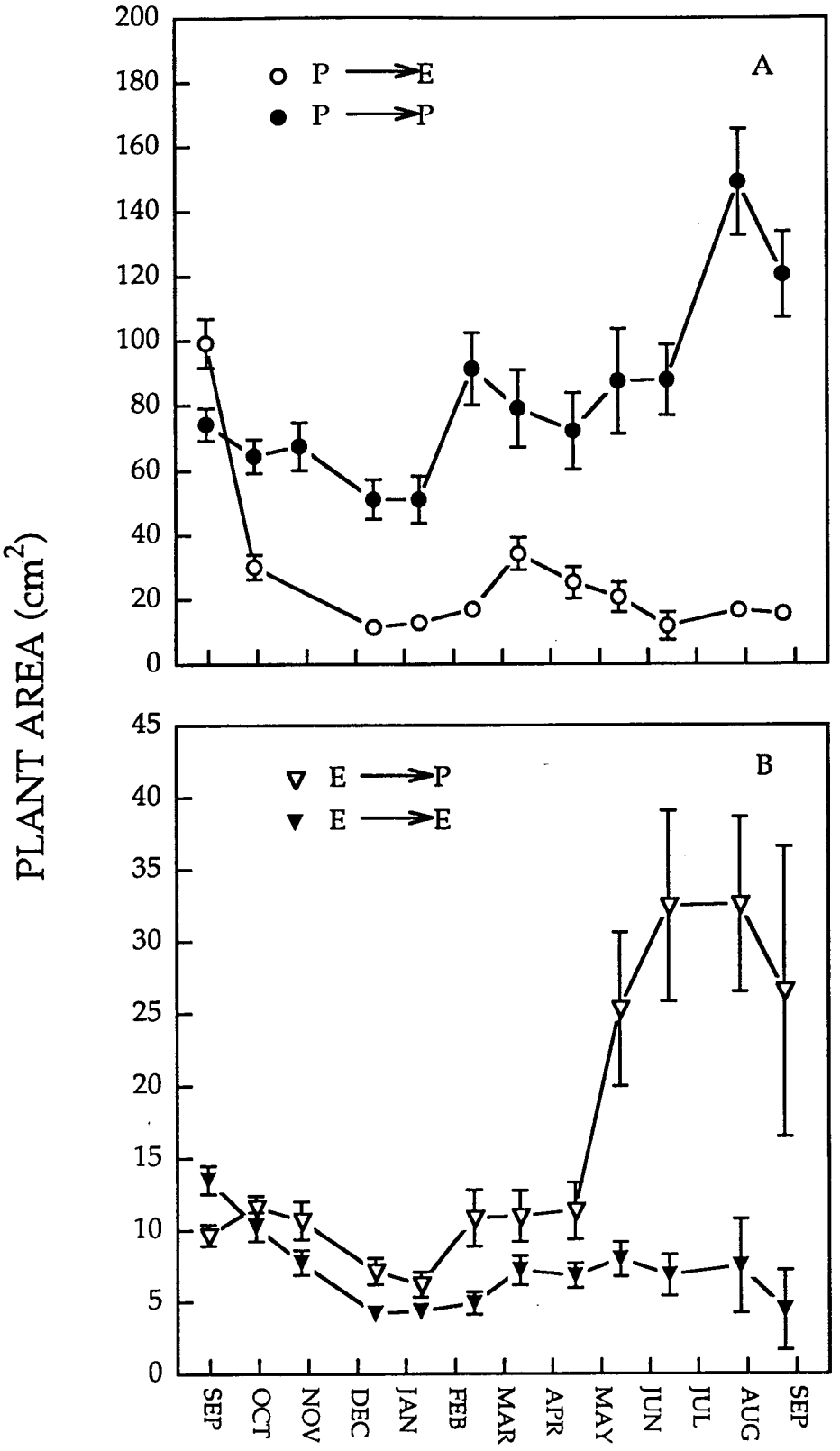

PLANT AREA (cm²)
200
180
160
140
120
100
80
60
40
20
0
P → E
P → P
A
45
40
35
30
25
20
15
10
5
0
E → P
E → E
B
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Figure II.16. Mean lengths of plants remaining in each treatment and control group over time ± 1 s.e.m. Treatment transplants are represented as open symbols and controls as closed symbols. Numbers of plants as in Fig. II.12.

Figure II.16

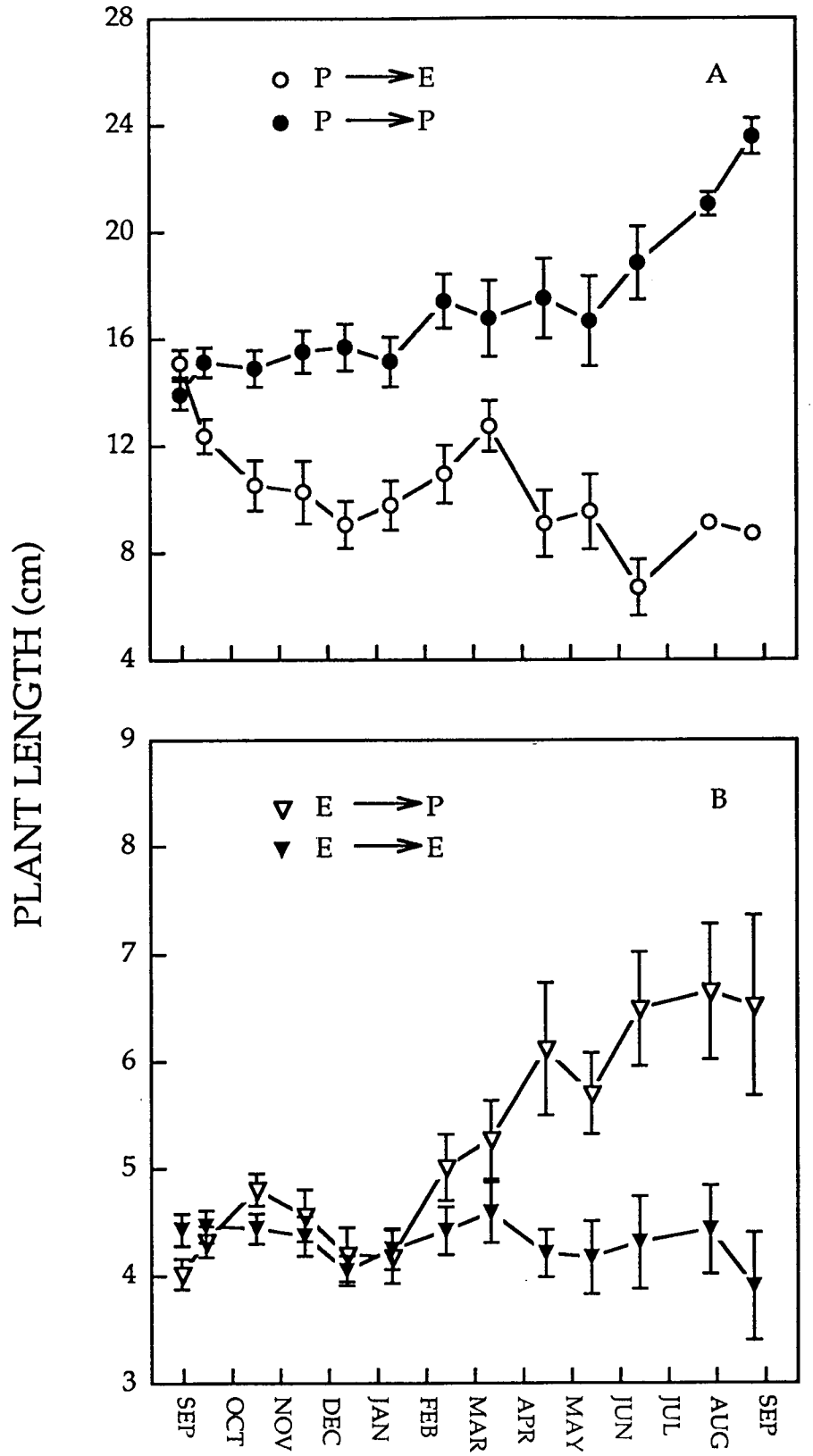

PLANT LENGTH (cm)
28
24
20
16
12
8
4
P → E
P → P
A
9
8
7
6
5
4
3
E → P
E → E
B
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Figure II.17. Monthly maximum areas (a) and maximum lengths (b) of experimental plants in each of the treatments (open symbols) and controls (solid symbols) over time.

Figure II.17

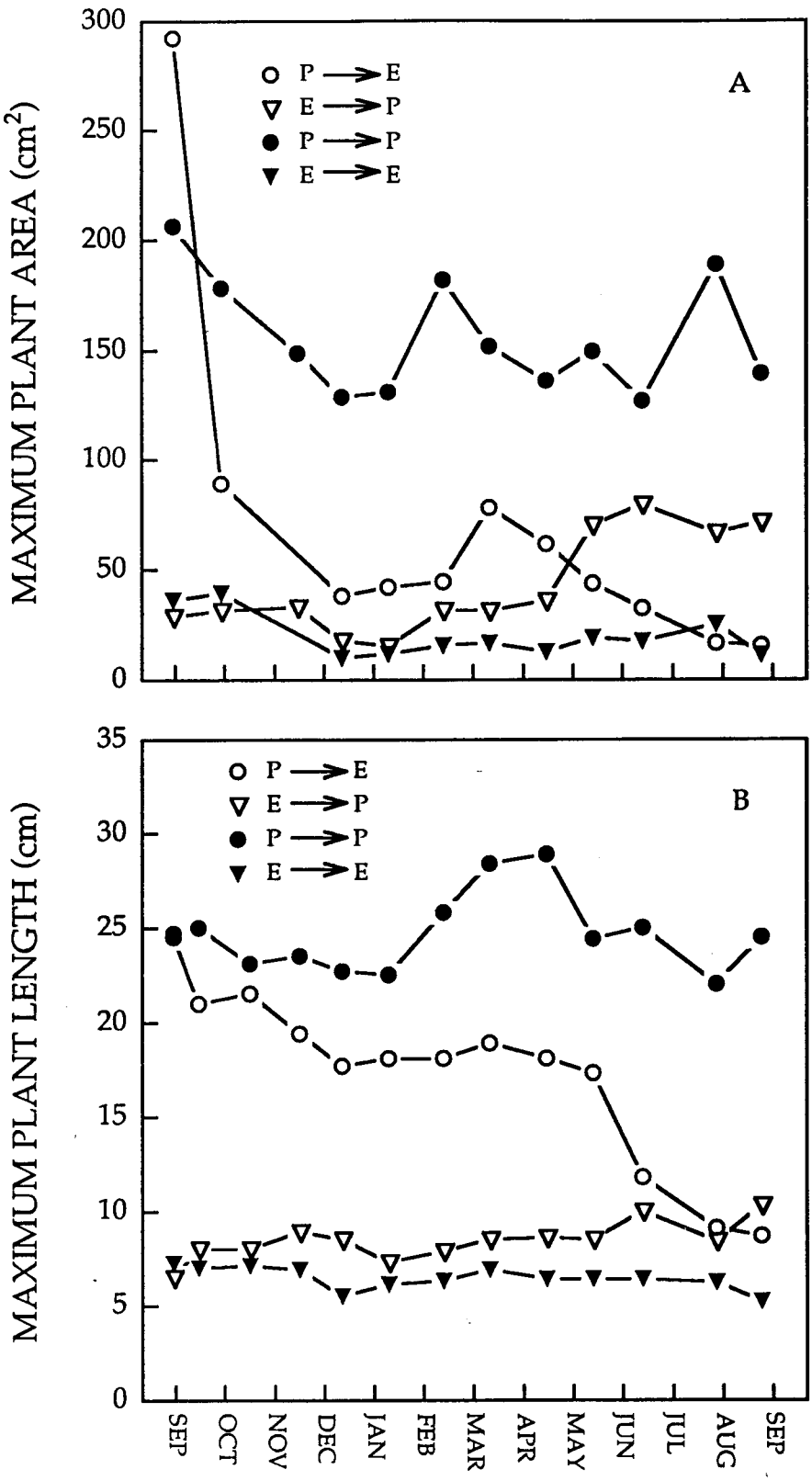

MAXIMUM PLANT AREA (cm²)
300
250
200
150
100
50
0
P → E
E → P
P → P
E → E
A
MAXIMUM PLANT LENGTH (cm)
35
30
25
20
15
10
5
0
B
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Figure II.18. Mean length ± 1 s.e.m. (a) and maximum length (b) of controls transplants (closed symbols) and tagged plants (open symbols) over time. Mean and maximum lengths of protected control plants did not differ significantly from protected tagged plants over time. Mean and maximum lengths of exposed control plants did not differ significantly from exposed tagged plants over time.

Figure II.18

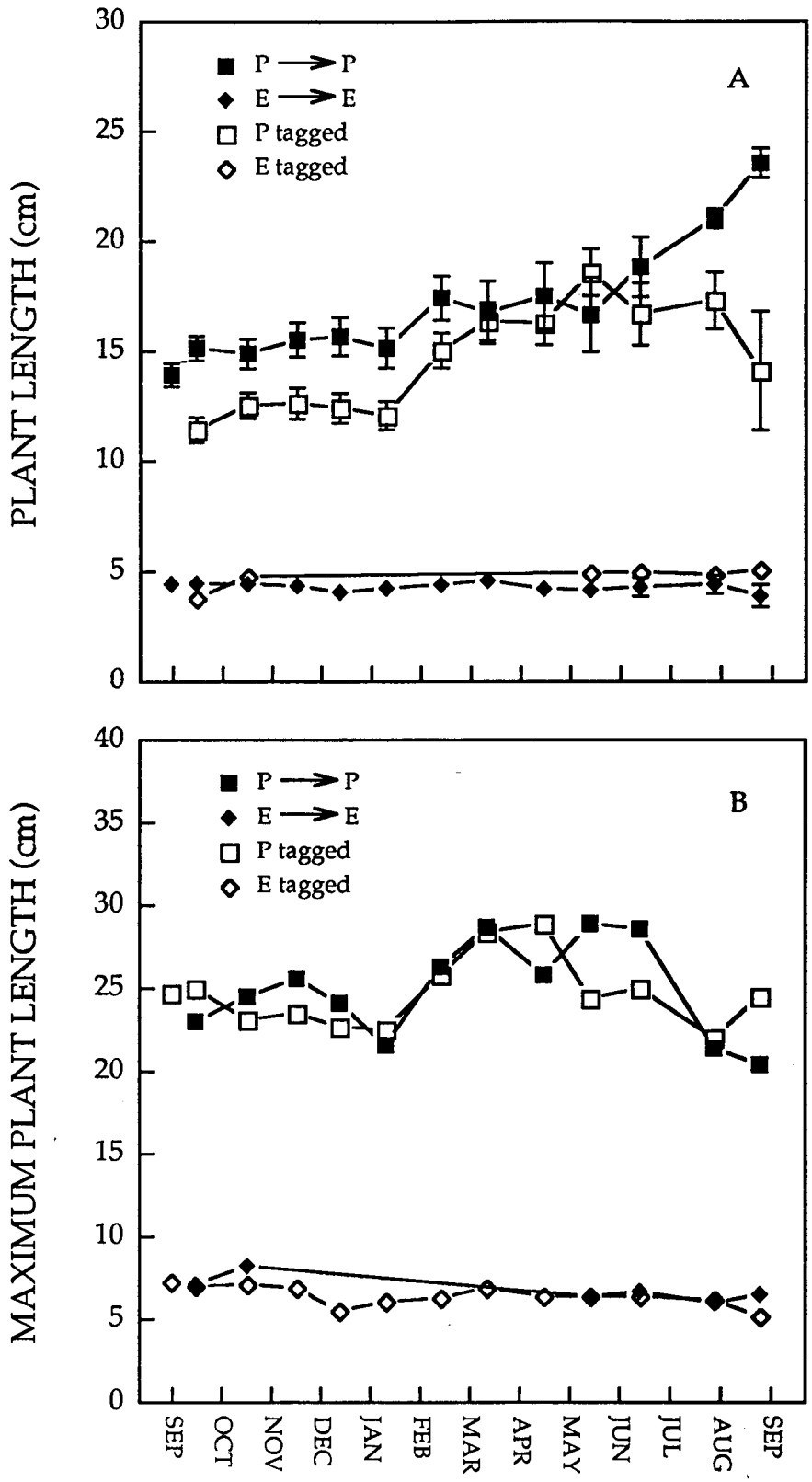

PLANT LENGTH (cm)
30
25
20
15
10
5
0
P → P
E → E
P tagged
E tagged
A
MAXIMUM PLANT LENGTH (cm)
40
35
30
25
20
15
10
5
0
P → P
E → E
P tagged
E tagged
B
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Figure II.19. Mean growth of plants which survived the experimental period from September 1992 to July 1993 represented as (a) change in area and (b) change in length ± 1 s.e.m.

Figure II.19

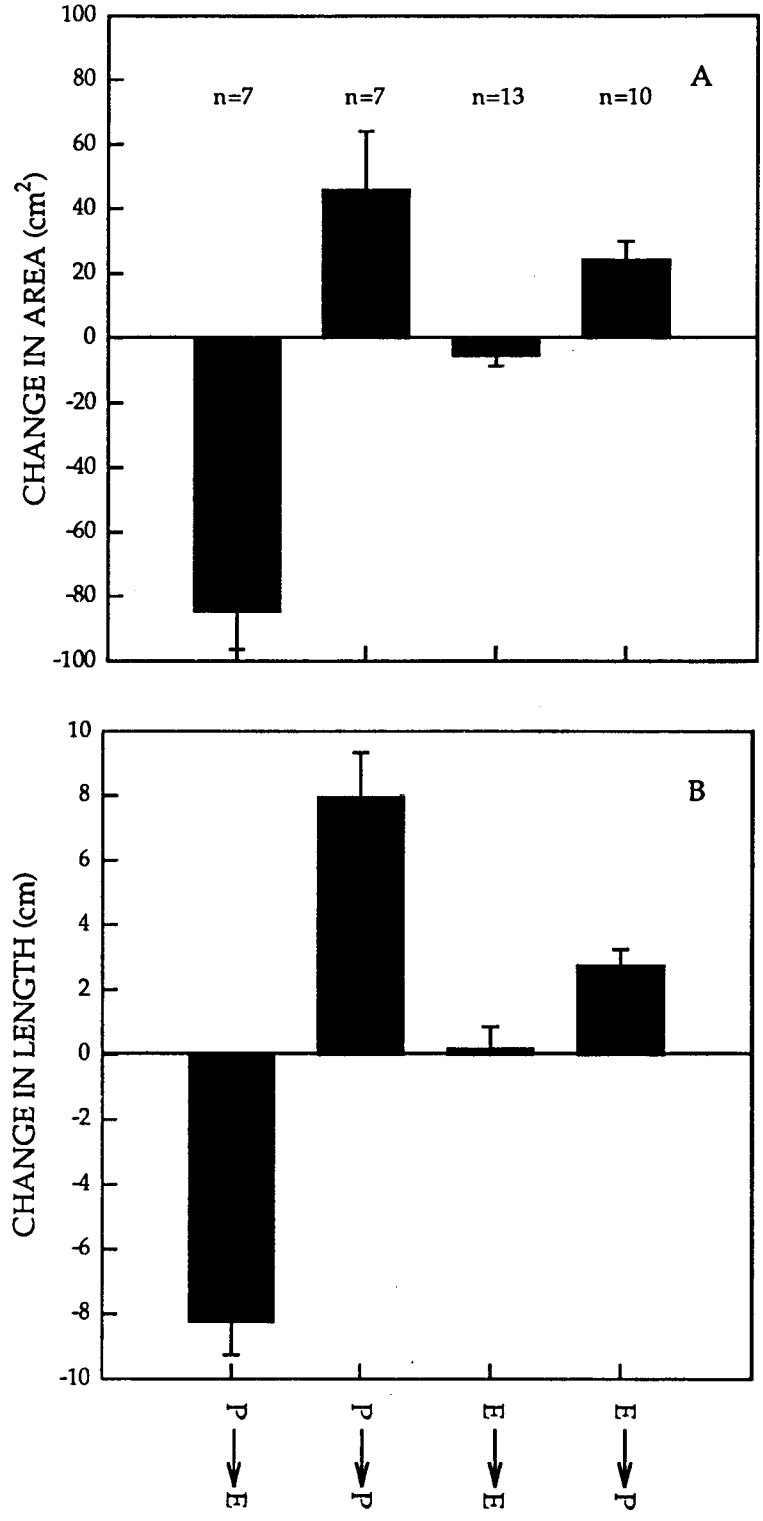
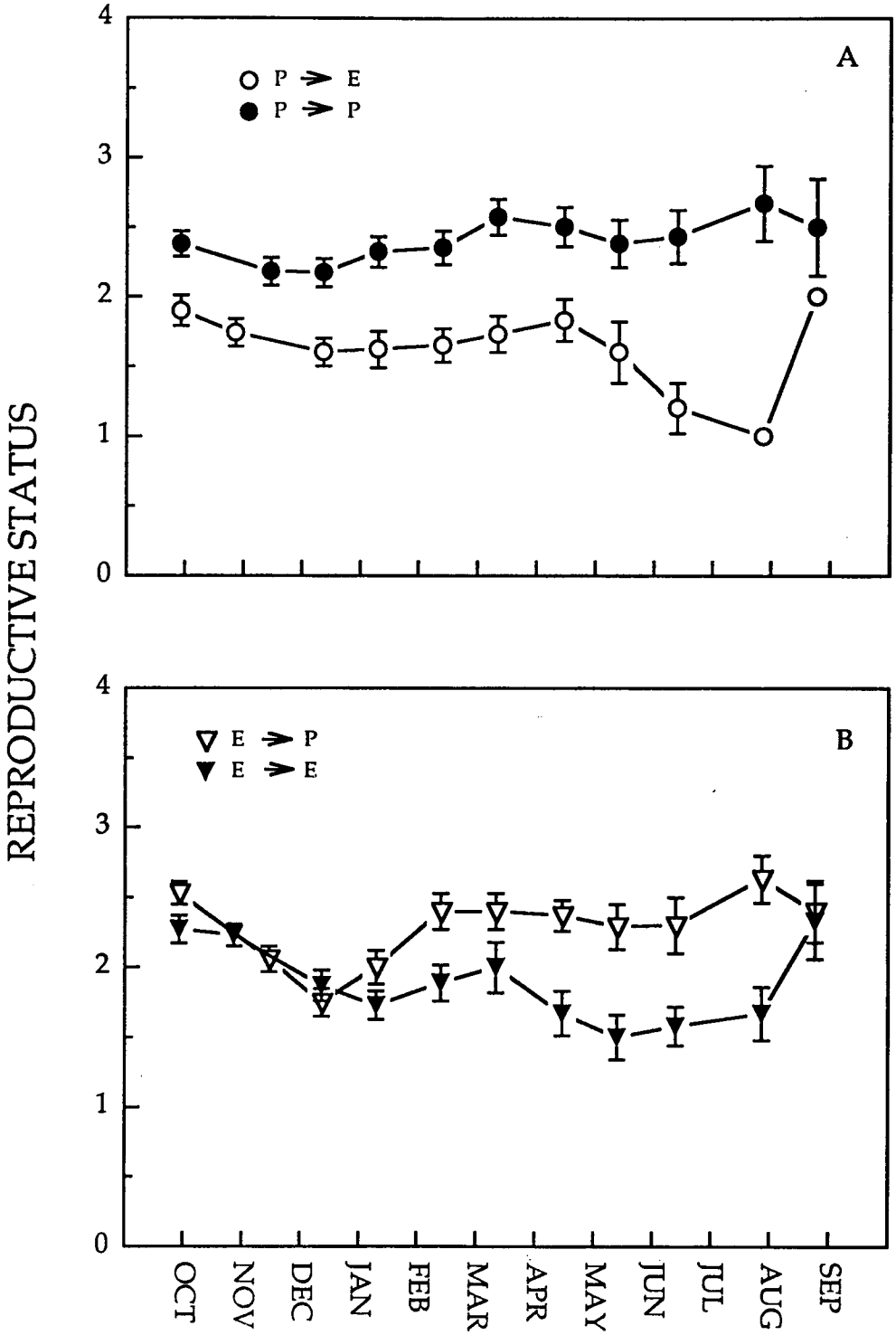

A
n=7
n=7
n=13
n=10
CHANGE IN AREA (cm²)
100
80
60
40
20
0
-20
-40
-60
-80
-100
B
CHANGE IN LENGTH (cm)
10
8
6
4
2
0
-2
-4
-6
-8
-10
P→E
P→P
E→E
E→P

Figure II.20. Mean reproductive status of experimental transplants (open symbols) and controls (solid symbols) ±1 s.e.m. Reproductive status of each plant was scored as the number of blades on each plant containing reproductively mature receptacles: 0=none, 1=few, 2=some, 3=many, 4=all.

Figure II.20


REPRODUCTIVE STATUS
A
P → E
P → P
B
E → P
E → E
0
1
2
3
4
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP

Chapter III

SEASONAL PATTERNS OF DISTURBANCE AND WAVE EXPOSURE INFLUENCE RECRUITMENT AND GROWTH OF THE SEA PALM, *POSTELSIA PALMAEFORMIS*

ABSTRACT

Despite many studies on disturbance, few have considered how temporal variation in physical disturbance may influence the abilities of species to persist or recruit at a site. This is particularly important for species that reproduce seasonally and for species with heteromorphic life histories, such as kelps. The sea palm, *Postelsia palmaeformis* is a kelp that inhabits the mid-tidal zones of the most wave exposed rocky intertidal areas on the Pacific coast from central California to Vancouver Island, B.C. Previous studies have shown that sea palm spores disperse only a few meters from adults and that populations of *Postelsia* can only persist in wave-exposed sites where disturbances of a large magnitude occur frequently. *Postelsia* thrives in wave beaten areas, since wave disturbances remove patches of *Mytilus californianus*, the dominant competitor, thereby freeing bare space on the rock where the spores of *Postelsia* survive and grow. The experiments in this study were designed to evaluate two main questions: (1) How does temporal variation in physical disturbance influence *Postelsia* recruitment at a site? (2) Are *Postelsia* physiologically restricted to wave exposed sites?

The effect of temporal variation in disturbances was studied by manually disturbing small plots around existing *Postelsia* patches in

different seasons. Mussels were removed from areas in (a) summer, when many reproductive adult plants were present; (b) winter, when no adult plants were present; and (c) winter, but additionally sterilizing the rock surface. I censused the number of sporophyte plants in these plots following the disturbances, and in mussel bed "control" plots monthly in the year following the manipulations. This experiment was repeated over two consecutive years. The tolerance of physical conditions by sea palms was tested by transplanting *Postelsia* from mid-zone, wave-exposed sites to high, mid and low zone sites at each of three levels of waves exposure: protected, intermediate and exposed.

Recruitment of sporophyte *Postelsia* did not occur in any of the treatments until the following spring. Sea palm recruitment occurred in all plots, but was greatest in the winter mussel removal treatment, suggesting that microscopic or young stages of *Postelsia* may be able to survive from summer to winter beneath mussel beds. Sea palm densities were also greatest in plots that were disturbed in the most recent winter. *Postelsia* at mid-zone wave-exposed and intermediate sites had the highest survival and growth rates. All wave-protected transplants and all high zone transplants had low survival and low growth rates, even in the absence of disturbance and competition for space with mussels.

Postelsia's restriction to wave exposed sites is due both to: 1) occurrence of predictable winter disturbances at these sites which remove *Mytilus*, thereby stimulating sea palm spore germination, gamete release or sporophyte growth from the underlying rock, and 2) high water motion which enhances sea palm growth presumably by increasing nutrient exchange and photosynthesis and preventing desiccation at low tide.

INTRODUCTION

Disturbances in natural communities occur over varying temporal and spatial scales and can affect the distributions and abundances of species living in many ecosystems (Sousa 1984, Pickett and White 1985). A disturbance may be defined generally as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment" (Pickett and White 1985). In this sense, both physical and biological processes may act as agents of disturbance (Harper 1977). Examples of physical disturbances include fires, floods, drought, high wind, large waves, ice scour and landslides. Biological disturbances range from grazing or predation to nonpredatory behaviors that may kill or displace other organisms (Sousa 1984). Influences of disturbances on community or ecosystem structure are strongly dependent on the rate of resource release, its timing, spatial scale, magnitude and periodicity (Levin and Paine 1974, Connell 1978).

Life cycles of many sessile organisms are strongly dependent on the occurrence of disturbance, since persistence of many sessile populations depends on dispersal to sites suitable for recruitment. A population will persist in a given area only if that area provides a sufficient number of suitable sites per unit time to guarantee successful recruitment during the adult's lifetime. A species whose offspring can survive and grow under environmental conditions similar to those experienced by the adults usually does not disperse its propagules far, and it potentially can persist in a relatively small area (Sousa 1984). Many species depend on disturbance

to create conditions favorable for the recruitment, growth and reproduction of their offspring. The pattern of recolonization following a disturbance can depend on the reproductive biology and life history traits of species that are on or within dispersal distance of the site, and characteristics of the disturbed patch including: the intensity and severity of the disturbance that created it, its size and shape, its location and degree of isolation from sources of colonists, the heterogeneity of its internal environment, and the time it was created (Sousa 1985).

Patch location and the proximity of a patch to sources of colonists are two factors that can greatly influence the mode and rate of colonization of a recently disturbed area, particularly for species that do not disperse their propagules very far (Dayton 1973, Platt and Weis 1977, Bormann and Likens 1979, Paine 1979, Horn 1981, Sousa 1984). The time at which a patch is created by disturbance will indirectly affect colonization if the availability of propagules varies over time (Kennelly 1987a, b, Reed et al. 1988, Reed 1990b). In systems where disturbances occur seasonally and where there are species with annual life histories, the time of patch creation is especially important.

The relationship between the time at which a patch is created and patch recovery may be even more complicated in systems that contain plants with heteromorphic life histories (e.g., kelps, ferns). In these plants recruitment includes the successful completion of a separate life history phase, the microscopic gametophyte stage (see Fig. III.1). Following release from the adult sporophyte, mobile zoospores settle and germinate into either male or female gametophytes. Gametophytes are sessile, free-living, microscopic plants, and when sexually mature, they produce eggs or sperm.

Following syngamy the sporophyte begins to develop. Thus sporophyte recruits in these plants are derived from an intermediate stage and are not the same individual as those that initially settled. In contrast to more advanced plants or sessile marine invertebrates, recruitment in primitive plants such as kelps may be influenced by post-settlement events which can occur in two very different life history stages: the sexual gametophyte or the asexual microscopic sporophyte. The biology of the gametophyte generation in kelps has been extensively studied (see Kain 1979, Bold and Wynne 1988): however, its ecology is poorly understood due to the small size of gametophytes and the difficulty of observing them in nature. Most studies on kelp recruitment have focused attention on the sporophyte stage (Sundene 1962, Dayton 1973, Paine 1979, 1988, Chapman 1984, Dayton et al. 1984, Harris et al. 1984, Reed and Foster 1984, Reed et al. 1988, Dean et al. 1989, Reed 1990b). The presence of microscopic forms such as the gametophyte stage that are alternate phases in the life history of macroscopic species and of propagules or spores that are in different degrees of development have led to an awareness of the common existence of a large unseen population of microscopic stages which are usually not identifiable (Santelices 1990). By analogy with the seed bank of land plants (Harper 1977), this microscopic algal population has been referred to as the bank of microscopic stages of seaweeds (Chapman 1986).

Theoretical studies of life history models also support the idea that seasonal environments are crucial in the evolution of life histories which have more than one ecologically distinct phase (Istock 1966). The orders of brown algae having heteromorphic life histories are poorly represented in tropical regions, and occur predominantly in temperate and polar latitudes

that are characterized by pronounced seasonal changes in the physical environment (Clayton 1988). Clayton (1988) suggests that seasonal factors such as winter disturbances have had an important selective effect on the evolution of heteromorphic life histories and that the different morphological phases have evolved in response to environmental change. Sporophytes of many species in the orders Chordariales, Dictyosiphonales and annual species of Laminariales have relatively short lifespans and commonly grow during the spring and summer. They shed their spores and degenerate before the onset of winter, while presumably the spores or gametophytes survive and/or grow in winter (Clayton 1988). We can only speculate on the adaptive significance of life histories in these orders, since there is very little experimental evidence to indicate which particular environmental factors have influenced natural selection.

In this paper I focus on how the disturbance regime of the wave-exposed intertidal zones of the northeast Pacific may influence the recruitment, growth and survival of the sea palm, *Postelsia palmaeformis*. *Postelsia* is a brown alga of the order Laminariales that lives in the middle and upper intertidal zones of wave-exposed shores. It ranges from central California to Vancouver Island, B.C. (Abbott and Hollenberg 1976). The sea palm is a kelp and has an annual, heteromorphic life history (Bold and Wynne 1988) (Fig 1). The macroscopic sporophyte is a conspicuous member of wave exposed, rocky areas in summer where it often forms large aggregations. In Oregon, the sporophyte begins to appear in January, grows rapidly through the spring and becomes reproductive in late spring/early summer. In summer the stipes of the sporophytes can reach sizes of 50-75 cm (Paine 1986, 1988). The hollow stipe supports a crown of

blades which function in both photosynthesis and reproduction. The spores are produced in longitudinal groves on blades and dripped onto the substrate at low tide and probably attach immediately and become microscopic gametophytes (Dayton 1973, Paine 1979, 1988). Experiments have shown that spores are capable of dispersing only a few meters from a sessile adult source (Dayton 1973).

The sea palm does not appear to be adapted for long-distance dispersal, but can successfully maintain populations in areas known to be subjected to intense competition for space, particularly from *Mytilus californianus* known to be a competitive dominant (Paine 1966, Dayton 1971, 1973). In horizontal or slightly sloping areas, *Postelsia* are often found in gaps in beds of *Mytilus*. Sea palms are often densely aggregated in these areas and are not often found growing on *Mytilus*. In this habitat, disturbances from wave action are relatively common, especially during winter storms. Waves can remove patches of mussels, thereby freeing primary space on the rock.

The ability of *Postelsia* to persist at a site is dependent on the occurrence of predictable disturbances above some threshold size and at a sufficient rate for *Postelsia* to occupy sites continually (Paine 1979, 1988). These disturbances remove patches of *Mytilus*, the dominant competitor, and renew bare rock space, judged by Paine (1988) to be the most suitable substratum for *Postelsia* recruitment and survival. *Postelsia* are not found in wave protected areas and apparently cannot persist in sites with low disturbance rates, since *Mytilus*, the dominant competitor, can over time move in and outcompete *Postelsia* if undisturbed (Paine 1979). *Postelsia* populations can persist by overgrowing and smothering competing

organisms such as mussels, barnacles and algae. Bare space is renewed when *Postelsia* grow to a large enough size that the forces of drag produced by large waves overcome the tenacity of the organisms to the rock. The sea palm, as well as the organisms it had overgrown are then ripped from the rock. In this scenario proposed by Dayton (1973), more *Postelsia* zoospores from adjacent plants can then settle and germinate in the summer on the space thus made available. This manner of recruitment is confusing in the context of *Postelsia*'s annual life history. Space made available by removal of mussels and other organisms in summer when sea palms are reproductive may be deluged with spores from neighboring *Postelsia*. However, it seems unlikely that these spores will go through the entire heteromorphic alternation of generations and appear on the rock as sporophytes in the same summer that the spores settle. Additionally, most disturbances to the mussel bed occur in winter during storms when reproductive *Postelsia* are no longer present. Thus recruitment of *Postelsia* sporophytes to these disturbed patches should not be apparent until the spring of a full year following the time of patch creation.

Two questions arise from present ideas about the relationship between disturbance, recruitment of *Postelsia* and survival of adults. 1) If disturbance occurs in winter, but reproduction occurs in summer when many disturbances have been colonized by sessile organisms or even closed by mussel encroachment, how do *Postelsia* come to dominate newly cleared patches in winter? 2) Why is *Postelsia* most abundant in mid-zone, wave exposed mussel beds, where space is least available, yet absent from wave protected sites lacking *Mytilus*?

In an attempt to understand how temporal variation in the disturbance regime and the degree of wave exposure influence the recruitment and survival of *Postelsia*, this study addressed the following specific questions:

1) Given that *Postelsia* is known to have a heteromorphic, annual life history and lives in an environment that is disturbed seasonally, how does the time of year at which a mussel clearing disturbance occurs influence the ability of *Postelsia* to recruit at a site?

2) Given that populations of *Postelsia* are not found in areas characterized by low disturbance and that *Postelsia* is outcompeted by *Mytilus* in the absence of disturbance, can *Postelsia* survive and grow in wave-protected sites characterized by low disturbance rates in the absence of competition by mussels?

METHODS

EFFECT OF SEASONAL DISTURBANCE

Natural seeding

To test the effect of season of disturbance on recruitment density of *Postelsia,* I initiated experiments in which clearances were made in mussel beds. In the first experiment (this section) I allowed clearances to be seeded with sea palm recruits naturally. In the second experiment (next section) I manually seeded plots. The first experiment was conducted at the South Point of Depoe Bay (SPDB) (44°49'N, 124°04'W) on the central Oregon coast. The site is a slightly sloping, rocky (basalt) headland fully exposed to oceanic waves. Experimental plots were located on a slightly sloping rock surface in the middle of the *Mytilus/Postelsia* zone. Island-like, small (50-100 plants) clusters of *Postelsia* are scattered throughout the mussel bed in this area. Occasionally *Postelsia* are found growing on the mussels, but most *Postelsia* are confined to these small clusters in the mussel bed.

To examine how the recruitment of *Postelsia* may be affected by the time of year at which a mussel-removing disturbance occurs, I initiated an experiment in the summer (July) of 1991 at SPDB. The experimental units were 45 cm x 45 cm plots marked at the corners with stainless steel screws. I established 16 plots in the mussel bed. All plots were within 0.5 m of a large *Postelsia* cluster and were all located in areas that were likely to be deluged with *Postelsia* spores during the summer reproductive season. I randomly assigned one of four treatments to each plot: 1) summer

disturbance; 2) winter disturbance; 3) winter disturbance and sterilization; and 4) no disturbance (unmanipulated) (Fig. III.2). For the summer disturbance treatment, I removed mussels from each plot in July 1991. In the winter disturbance and winter disturbance plus sterilization treatments, I removed mussels from each plot in December 1991 when there were very few remaining adult *Postelsia* at the site. Any remaining adult *Postelsia* that were within 25 m of the plots were also removed in winter. In the winter disturbance plus sterilization treatment, I additionally "sterilized" the rock in each plot following mussel removal in an effort to eliminate microscopic algal spores. Sterilization was accomplished by scraping each plot with a stiff wire brush and chiseling 0.5 - 1 cm of rock off the top layer of each plot. The experiment was repeated in summer (July) 1992, using the same method for the new summer and winter disturbance plots. In addition to re-chiseling the winter disturbance plus sterilization plots, two coats of oven cleaner were applied to each of the plots in an attempt to kill microscopic algal forms hidden in cracks in the rock.

To avoid edge effects, the inner 0.16 m^2 of each plot was sampled. Number of *Postelsia* in each plot were recorded each month in the year following the experiment. I also recorded the number of *Postelsia* in each plot monthly in 1993 from the winter and summer disturbance 1991 plots. Data analysis employed repeated measures analysis of variance. I visually examined residual and normal probability plots and log transformed the density data to achieve approximate normality. Seasonal effects of clearing and the effects of sterilizing rock on *Postelsia* densities were determined using multiple contrasts within the repeated measures analysis.

Manual seeding

The second experiment was conducted at Fogarty Creek Point (FCP) (44°51' N, 124°03'W) on the central Oregon coast (see chapter II for site description). Experimental plots were located on a wave-exposed mussel bed area that lacked dense *Postelsia* (except for 8 plants in one small patch of bare rock), yet seemed similar in tidal height and wave exposure to sites where *Postelsia* was present. The mussel bed in this area was extremely thick in places (0.2 m - 0.4 m thick). I initiated the experiment in summer (July) 1992 similar to that at SPDB, using the same treatments as those previously described: 1) summer disturbance; 2) winter disturbance; 3) winter disturbance and sterilization; and 4) no disturbance (unmanipulated). To more tightly control *Postelsia* recruitment, I used a method similar to the *Postelsia* seeding procedure described by Paine (1988). I fashioned 16 0.25 m^2 baskets out of chicken wire and filled each with the bladed portions from 10 reproductively mature *Postelsia* (Fig. III.3). I strapped each *Postelsia* filled basket over each plot using 4 - 8 stainless steel eyebolts and plastic cable ties. Additionally, I picked 10 reproductively mature *Postelsia* and swirled their fronds in a 5-gallon bucket of fresh water to stimulate spore release (Paine, 1988). I then poured approximately 1 l of this mixture over each plot. After two months I removed the partially mangled baskets, many of which still contained shredded *Postelsia* material.

As in the SPDB experiment, I counted the number of *Postelsia* in each plot monthly in 1993. Two of the plots assigned to the

unmanipulated treatment were naturally cleared of mussels by winter storms. Due to extreme variance within treatments, I did not statistically analyze the data and I present a table of the raw results in the results section.

EFFECT OF LOCAL ENVIRONMENTAL CONDITIONS

Transplants, seedings and common garden experiments have been commonly employed to evaluate the ability of a species to persist and/or grow in a given area (Druehl 1967, Pollock 1969, North 1971, Rabinowitz 1978, Schonbeck and Norton 1981, De Paula and De Oliveira 1982, Sideman and Mathieson 1983, 1985, Paine 1988, Chapman and Johnson 1990). Transplants were the method of choice in this investigation to assess the ability of *Postelsia* to survive and grow in areas where they are not normally found.

To determine if *Postelsia* are able to survive and grow at wave-protected sites or at areas above or below the main *Postelsia* zone, I transplanted *Postelsia* (10 plants in each group) from a mid-*Postelsia* zone wave exposed site to high, mid and low zone sites at each of three levels of wave exposure. These were a wave-exposed site (where *Postelsia* were present), an intermediate wave exposure site (where *Postelsia* were also patchily present) and a wave-protected site (where no *Postelsia* were present) all at SPDB selected on the basis of observations of wave patterns. To transplant *Postelsia*, I chiseled 10 large holes (4 cm - 6 cm deep and approximately 5 cm wide) into the rock in the middle zones (middle of the *Mytilus/Postelsia* zone), lower edges of the high zones (*Iridaea*

cornucopia/Fucus gardneri zone), and upper edges of the low zones (*Phyllospadix/Corallina* zone) at each site. *Postelsia* to be transplanted were collected from a 25 m transect in the middle of the *Postelsia* zone in a wave-exposed, *Mytilus*-dominated area in April. I collected all small *Postelsia* (3 cm - 6 cm) that were growing on medium-sized *Mytilus* (4 cm - 6 cm) and were within 1 m of the tape. *Postelsia* were transplanted to each of the 9 sites by gluing the mussel (to which the *Postelsia* was attached) into the pre-chiseled hole using marine epoxy putty (Z Spar, Kopper's Co., Los Angeles). I labeled each transplant using a numbered plastic label pressed into the putty (Fig. III.4). The 10 mid-zone wave-exposed *Postelsia* were transplanted to holes at the same site from which they were collected, and were the "control" transplants. Locations of all transplants were also mapped since the haptera of the *Postelsia* holdfasts grew over the putty and obscured the numbered tags within a few weeks to months following the transplants.

Relative wave exposure at each area was measured using maximum wave force dynamometers (see chapter II for description). Three dynamometers were placed in the high, mid and low zone at each site on each date. I recovered the meters after 24 hours and recorded the measurements.

Transplants were censused each month. Stipe length, basal stipe width, number of blades and length and width of four randomly chosen blades were measured for each individual. Although all plants eventually broke or were ripped out by waves, the mussel to putty adhesion held in all cases. Due to the high mortality of plants in wave-protected and high zone treatments beyond the first few months, data from only the first three dates

of the experiment could be analyzed using a repeated measures analysis of variance.

For comparative purposes, I also attempted to mark unmanipulated plants. Unfortunately, no method was successful. Preliminary tagging of several randomly chosen *Postelsia* at the mid-zone wave-exposed site using either fish tags (Floy Tag Co., Seattle, WA) or bird bands (National Band and Tag Co., Newport, KY) was unsuccessful for various reasons. In the first few months, the plants grew so rapidly that the tags had to be changed every month to a larger size. Tags placed loosely on the plant were stripped off by waves. Tags attached to: blades were lost, holdfasts were overgrown, and stipes were severed causing the plant to break. Marks made on the rock were rapidly overgrown by holdfasts, and mapping of plants was useless in dense, rapidly growing aggregations and was very time consuming.

Since I could not reliably tag natural plants to measure growth, I chose ten plants from the each of the tidal zones at the wave exposed site for measurement in August. The ten highest and ten lowest plants (with respect to tidal height) that I could find along a 25 m transect were chosen and compared with ten randomly sampled plants from the mid zone. Sizes of these naturally growing plants were compared to the sizes of wave exposed transplants in each of these zones. Since there were no high zone transplants remaining in August, I used data from the high zone transplants in July for comparison.

RESULTS

EFFECT OF SEASONAL DISTURBANCE

First year (1992)

Postelsia first began to appear in the experimental plots in February and persisted through September (Fig. III.5). No *Postelsia* appeared in the summer plots immediately following summer mussel clearings. There was large variation in *Postelsia* densities within treatments and the treatment effect in the repeated measures analysis of variance was not statistically significant (Table III.1). There were also no significant differences between treatments over the course of the experiment. On average, plots in which mussels were removed in winter had the highest *Postelsia* densities. Plots that were cleared of mussels in winter and scraped and chiseled had lower *Postelsia* densities than plots that were cleared in winter and not scraped. Plots that were cleared of mussels in summer had densities similar to those that were cleared of mussels and scraped in winter. Plots that were not cleared of mussels had the lowest *Postelsia* densities.

Second year (1993)

In the second experimental year at SPDB, *Postelsia* first appeared in the plots in February and persisted through November (Fig. III.6). No *Postelsia* appeared in the summer plots immediately following summer

mussel clearings. Plots in which mussels were removed in the winter had the highest densities of *Postelsia* in the following year. Plots that were cleared of mussels in the summer had lower densities of *Postelsia* than those cleared in winter, but significantly higher *Postelsia* densities than unmanipulated plots. *Postelsia* densities varied significantly depending on both the experimental treatment and census date (Table III.1). The first and last dates (February, October and November) were not included in the analysis since *Postelsia* densities are very low both early and late in the season. The effect of sterilizing was highly significant, and plots that were cleared of mussels in the winter and sterilized had far lower densities of *Postelsia* than those that were cleared and not sterilized. Unmanipulated plots had slightly higher densities of *Postelsia* than sterilized plots, though these differences were only statistically significant in March and July.

Plots that were cleared of mussels in 1991 were monitored in 1993 as well as 1992. Plots that were cleared of mussels in the most recent winter (1992) had significantly higher densities of *Postelsia* in 1993 than plots that were cleared of mussels in the previous winter (1991) (Fig. III.7, Table III.2). There were no significant differences in the densities of *Postelsia* in 1993 between plots cleared of mussels in summer 1991 and summer 1992. Plots cleared in the winter of 1991 had, on average, higher *Postelsia* densities than plots cleared in the summer of 1991 though these differences were not statistically significant. Plots that were cleared of mussels in the winter of 1992 had significantly higher densities of *Postelsia* than those cleared in summer of 1992.

In summary, mussel bed areas that were disturbed in winter, when no reproductive plants were present, had significantly higher densities of

Postelsia than areas disturbed in summer, which were surrounded with fertile plants. Areas most recently disturbed had greater sea palm densities than areas that had been free of mussels for several seasons. Scraping, chiseling and applying oven cleaner to the rock in winter reduced, but did not eliminate *Postelsia* recruitment in spring.

Manual seeding

Within-treatment densities of *Postelsia* were highly variable and could not be statistically analyzed (Table III.3). Two of the plots that were assigned to be unmanipulated controls (plots 1 and 4, Table III.3) were naturally cleared of mussels by winter storms. Several of the plots that were in areas with very low slope (i.e., horizontal) and surrounded by mussels did not drain well during low tides and tended to hold water in pools. *Postelsia* do not often settle or grow in pool areas (personal observation) and *Postelsia* never recruited in these plots. In well drained plots with higher slope angles, the seeding technique was very successful, and there is presently a very dense *Postelsia* aggregation at this site which has spread out from *Postelsia* in these plots over the last year (June 1994).

EFFECT OF LOCAL ENVIRONMENTAL CONDITIONS

Wave forces

Mean maximum wave forces were highest on all dates at the exposed site and were lowest at the protected site, and wave forces varied

depending on the wave meter location (site) (Fig. III.8, Table III.4). Maximum wave forces at the intermediate site were less than those at the exposed site, on average. Maximum wave forces at the intermediate site were greater than those at the protected site, though this difference was only significant in September. Maximum wave forces at the exposed site were significantly greater than those at the protected site in June, July, August and September. The maximum wave forces measured in this experiment are an underestimate of the actual maximum wave forces at the site, since I chose calm days during low tide periods for the monthly sampling.

Survival

Survival of plants transplanted to both high areas (at all exposures) and protected areas (at all tidal heights) was extremely low, and all transplants at these sites were gone by August (Fig. III.9). Transplants at both wave exposed (mid and low zone) and intermediate sites (mid and low zone) survived through October. I used a Logrank statistic to compare proportional survival and expected mortality of transplants both within tidal heights and wave exposures. Proportional survival of transplants within any tidal height did not differ between wave exposure sites over the course of the experiment (Table III.5). In contrast, survival of transplants within all wave exposure sites was significantly different among tidal heights. These results suggest that within a given tidal height (ex. the high zone), transplant survival did not depend on the degree of wave exposure.

However, within a given wave exposure site (ex. the wave-exposed site) transplant survival was significantly affected by tidal height.

Stipe length and width

As an indication of plant growth and performance under experimental conditions, I compared stipe heights, stipe widths and total blade surface areas among transplants at all tidal heights and wave exposures for the first two months of the experiment using a repeated measures analysis of variance. In the first two months, transplants at the different sites grew (in terms of stipe length and width) at different rates (significant tidal height x date and wave exposure x date interactions) (Table III.6). Stipe length was significantly affected by both tidal height and wave exposure, and stipe width was significantly affected by tidal height. Plants in the wave exposed and intermediate mid zone sites reached the largest stipe lengths, and also the largest stipe widths (Figs. III.10 & 11). Plants in the high zone at all wave exposures were gone by August and grew very little in the first few months. Plants in the low zone at intermediate and exposed sites reached stipe lengths that were approximately half the size of those at mid zone sites, but stipe widths were approximately equal to those at mid zone sites. The ratio of stipe length to stipe width resulted in short, stout looking plants in the low zone.

Total blade surface area

Total blade surface area was calculated by multiplying twice the average blade area (assuming an elliptical shape and using blade length and width measurements from four randomly chosen blades from each plant) by the number of blades on each plant. This provided an estimate of photosynthetic surface area and reproductive capacity. Total blade surface areas varied depending on the sampling date and tidal height (Table III.6). Mid zone wave exposed and intermediate plants had very high blade surface areas in mid summer (Fig. III.12). Low zone intermediate plants had very high blade surface areas in late summer, and these were approximately twice as large as those of low zone, exposed plants. High zone plants at all sites did not develop any significant canopy.

Transplants versus naturally occurring *Postelsia*

Postelsia transplants closely matched the sizes of naturally growing *Postelsia* found in wave exposed high, mid and low zones in August (Fig. III.13). Stipe lengths, stipe widths and total blade surface areas were all greatest for mid zone plants, less for low zone plants and least for high zone plants, and all the plant measurements varied significantly depending on tidal height (Table III.7). Stipe length and width were significantly affected by plant type (natural or transplant), however there were no significant effects of plant type on total blade surface areas.

DISCUSSION

The wave-exposed rocky intertidal shores of the Pacific Northwest are characterized by high degree of competition for space (Connell 1961, Paine 1966, 1974, Dayton 1971, Paine and Levin 1981). Disturbances, due to drift logs and wave action are important events in removing competitively dominant species such as the mussel *Mytilus californianus* (Dayton 1971, Paine and Levin 1981). Sea palms that live in wave-exposed areas where *Mytilus* are present rely on some degree of disturbance to remove mussels and renew bare space on the rock (Dayton 1973, Paine 1979, 1988). The results of the *Postelsia* spore release and seeding experiments suggest that *Postelsia* can settle on and survive on mussels, but only at very low densities. Dayton (1973) proposed the following mechanisms for the lack of *Postelsia* recruitment on *Mytilus*: (1) filtration and ingestion of spores by *Mytilus*, (2) mortality of spores and gametophytes due to siltation and grinding among adjacent *Mytilus* individuals, (3) chemical antibiosis of *Mytilus* on *Postelsia*, and (4) a grazing effect of the limpets occurring on the *Mytilus* valves. Like Dayton, I am not convinced that any of these mechanisms alone can explain the observed patterns of limited recruitment of *Postelsia* on *Mytilus*. The fourth mechanism (grazing effects of limpets on the *Mytilus* valves) probably holds the most merit. *Lottia digitalis* and *Lottia pelta* both occur at very high densities on the valves of *Mytilus*. *Lottia pelta* sampled from a *Postelsia* zone site have been shown (through gut analysis) to consume large quantities of *Postelsia* at these sites relative to the amounts of available algae (Craig 1968). Limpets have also been shown to have significant negative effects on

Postelsia densities, particularly at the gametophyte and young sporophyte stages, where these plants can be entirely consumed by limpets (see Chapter IV).

An additional mechanism could explain not only the low level of *Postelsia* recruitment to *Mytilus* valves, but also the intriguing results in Dayton's 1973 experiments where *Postelsia* sporophytes suddenly appeared at sites in mid summer, immediately following an early summer mussel removal. I hypothesize that the large numbers of *Postelsia* spores which deluge mussel bed areas may, for the most part, dribble down through the *Mytilus* valves and settle on the rock beneath the mussel bed, leaving only some of the spores to actually settle on the valves of *Mytilus*. Of these spores that settle on *Mytilus* valves (and/or gametophytes and sporophytes that form from these spores), some are probably consumed by limpets, some are probably killed by desiccation and high temperatures on the black, quick heating valves of *Mytilus*, and some survive and appear as young sporophytes in the following spring. Spores that settle beneath the mussel bed and survive to the gametophyte stage may overwinter and reproduce in this dark, cool environment. Disturbances which typically remove areas of mussel beds in winter provide light and open space in these areas in spring, perhaps stimulating sprore germination, gametogenesis or the growth of the young sporophytes.

Spore germination in many species is a seasonal phenomenon, and several different ecological factors seem to be involved in germination (see Santelices 1990 and Brawley and Johnson 1992 for reviews). Barilotti and Silverthorne (1972) found temperature to be an important factor in the germination of *Gelidim robustum* spores from Baja California. Several

properties of light such as photoperiod, spectral quality and irradiance levels may affect gametogenesis in seaweeds, though elevated irradiance or direct exposure to sunlight may be generally damaging or lethal (Jones 1959, Burns and Mathieson 1972). Blue light is necessary for gametogenesis in some kelps (Luning and Dring 1972), and irradiance levels must exceed certain thresholds in *Desmarestia* (Chapman and Burrows 1970), and many laminarians (Luning and Neushul 1978, Luning 1980, Deysher and Dean 1984, 1986, Novaczek 1984). Nutrient levels may have some effect on gametogenesis, and it is known that nitrogen is required for gametogenesis in *Laminaria* (Hsiao and Druehl 1973). Gamete release also commonly occurs following a change in irradiance (Hollenberg 1935, Smith 1947, Muller et al. 1985). *Laminaria* release gametes within a few minutes of the beginning of the dark cycle when gametophytes are grown in the laboratory (Tseng et al. 1959, Luning 1981). Most studies on the effect of illumination on gamete release have been done in the laboratory, and little is known of the factors important in the field. Gametes that show phototaxis whether positive or negative might be presumed to be released more often during day than night in nature, however sperm of the Laminariales lack an eyespot and are not phototactic, so there is no apparent disadvantage to sperm release during light or dark periods.

Spore germination usually takes place soon after attachment in most macroalgae (Fletchier and Callow 1992) however, dormancy may occur after initial settlement, as in the brown alga *Dictyota* (Richardson 1979). The possibility of persisting as a microscopic form with suspended growth is generally recognized as an adaptation of the algae to survive through conditions stressful for the macroscopic thallus (Santelices 1990). This idea

has been explored in the young and microscopic stages of Laminariales. In the field the kelps frequently shade their own recruits. Measurements of light intensities in *Macrocystis* (Clendenning 1961) and *Laminaria* (Kain 1966, Smith 1967) forests have found intensity values far below the optimum required for active growth of young sporophytes. Anderson and North (1969) concluded that bottom light intensities could be limiting for growth about 50% of the time, but without preventing kelp establishment. Perhaps these low light conditions allow survival, but suspended growth and development of the microscopic stages thereby permitting persistance until the limiting conditions change and growth can be resumed (Santelices 1990). In *Desmarestia aculeate* the development of microscopic gametophytes produced in winter is suspended until spring when the light irradiance increases (Chapman and Burrows 1970). In other algae, the time of suspended growth can vary from a few days to several months. Schonbeck and Norton (1980) have reported finding viable microscopic *Pelvetia* germlings beneath adult stands of the same species 8 months after the end of the fertile season.

In experiments where Dayton (1973) removed patches of mussels in late spring/early summer in areas close to existing *Postelsia* patches, he observed the apparent recruitment of large densities of *Postelsia* in mid summer. Since only some *Postelsia* have reached reproductive sizes by late spring, it seems unlikely that these few reproductive plants would be able to seed an area in such a short time and the spores released in this area would be able to complete the entire heteromorphic life history (i.e., go from spores to gametophytes to sporophytes) in such a short time. It seems more likely that gametophytes and young sporophytes already present

beneath the mussel bed (derived from the previous summer's generation of reproductive plants) could quickly grow to visible sizes following the removal of this overlying mussel layer and the exposure to light.

Results of the spore release experiment at SPDB support this explanation. Young sporophytes appeared in plots in February, following the removal of mussels overlying these plots in winter, when there were no longer any reproductive *Postelsia* at the site to seed the recently disturbed areas. Plots cleared of mussels in winter (the time of year at which most natural disturbances occur) had the highest densities of *Postelsia* in the following year (Figs. III.5 & III.6). Plots cleared of mussels in mid/late summer made bare space available at a time when older *Postelsia* were reproductively mature. These plots had significantly higher densities of *Postelsia* in the following year than undisturbed plots, but had significantly lower *Postelsia* densities than plots disturbed in winter (Figs. III.5 & III.6). Also, plots that were cleared of mussels in the most recent winter had higher *Postelsia* densities than other plots cleared in previous summers and winters (Fig. III.7). This result suggests that the overlying cover of mussels may have a protective effect on young *Postelsia*. There are two possible mechanisms for this protective effect; (1) the environment under the mussel bed is dark and cool and probability of desiccation is low, while gametophytes or spores that are in open plots in late summer are exposed to the potentially adverse effects of the sun (heating, ultraviolet radiation, desiccation), and (2) limpets are relatively common on open surfaces in the *Postelsia/Mytilus* zone during most of the year and particularly in fall, and while limpets are common on valves of *Mytilus*, they are relatively uncommon on the rock beneath the mussel bed

(personal observation). Thus, the layer of rock beneath the mussel bed may therefore act as a refuge from physical stress, grazing or both. Contrary to the conclusions of Dayton (1973) that *Mytilus* exerts a strong negative influence on recruitment of *Postelsia, Mytilus* may actually enhance recruitment of *Postelsia* in areas that are subject to frequent disturbance, but negatively affect subsequent growth in the absence of disturbance. Therefore *Mytilus* can have a positive effect on *Postelsia*.

It is unclear why no *Postelsia* sporophytes were apparent in the summer disturbance plots in the late summer/fall immediately following the clearing. The summer disturbances were purposely done in late summer to insure that most of the adult plants surrounding these plots would be reproductive. However, this may have been too late in the season to stimulate germination of plants beneath the mussel bed.

Appearance of *Postelsia* in plots that were sterilized (by scraping, chiseling and oven cleaner application) suggests that the spores/gametophytes of *Postelsia*: (1) are extremely hardy, (2) can actually bore into the rock, (3) can disperse at the spore or gametophyte stage; or (4) are partly resistant to my sterilization technique. While I am convinced that the plants are extremely hardy at this stage, I am also convinced that there is some secondary dispersal at either the spore or gametophyte stage. Spores of brown algae are mobile (spores of brown algae are also referred to as zoospores), and it is unknown how long the spores can persist before germination to the gametophyte stage. Reed et al. (1992) found that spores of both *Macrocystis pyrifera* and *Pterygophora californica* could not swim longer than 120 hours, but though they were no longer actively swimming, they retained their capacity to produce viable sporophyte recruits.

Although many species of brown algae have been cultured in the lab, the time of germination is likely to be variable in nature, particularly if germination takes place beneath a mussel bed.

Male gametophytes must release sperm to fertilize female gametophytes and it is unclear how far the sperm of male gametophytes can travel. If the sterilization technique in this experiment was effective and the gametophytes can disperse, than both the male and female gametophytes must be capable of movement at this stage. The female gametophyte is typically sessile and is fertilized by the motile sperm in kelps (van der Meer and Todd 1980). Some eggs and/or zygotes may not be retained on the female gametophyte under all natural conditions, in contrast to observations made in the laboratory (Brawley and Johnson 1992). Dispersal at the spore, gamete, gametophyte and/or sporophyte may also occur via animal vectors. Algal spores have been observed on the legs and shells of amphipods and other invertebrates and some invertebrates also consume the reproductive tissue of algae, sometimes preferentially (Buschman and Bravo 1990, Santelices 1990). Spores can also survive digestion by invertebrates such as limpets. Experiments indicate that algal fragments contained in the fecal pellets from herbivores may have some ecological advantages over free propagules due to the sticky nature of the fecal pellet, protecting it from desiccation and allowing it to attach securely to the substratum (Santelices and Paya 1989).

At wave-exposed sites, the time at which disturbance occurs has an important effect on the recruitment of *Postelsia*. The annual, heteromorphic life history of *Postelsia* seems ideally suited to life in a seasonally disturbed environment, where winter storms can remove its

primary competitor, *Mytilus*. *Postelsia* is thought not to be found in wave protected areas characterized by low disturbance rates, since it can be outcompeted by *Mytilus* at these sites (Paine 1979). Although *Postelsia* are often found in association with *Mytilus*, sea palms also occur at sites where *Mytilus* are not present (see Chapter IV). *Postelsia* that are found along vertical or sloping rock faces are often found in association with an understory community of "turfy" algae, and are not in direct competition with *Mytilus*. An alternative explanation to describe why *Postelsia* are not found in wave protected areas may be that their growth and or survival is otherwise restricted at these sites. Water motion enhances the growth of aquatic organisms (Leigh et al. 1987) and in general, the productivity of marine and freshwater plants is higher in moving than in still water (Conover 1968). The brown alga *Hedophyllum* recovers from removal experiments within a year at the wave-exposed site of Tatoosh Island (Paine 1984) while it takes longer than 3 years at a nearby wave protected site in the San Juan Islands (Dayton 1975, Dethier and Duggins 1988). However increased exposure does not always increase productivity. In Chile, the kelp *Macrocystis* grows best at intermediate levels of exposure (Dayton 1985), and in Nova Scotia the kelp *Laminaria* also grows best in more sheltered locations (Gerard and Mann 1979).

In the transplant experiment, *Postelsia* had the highest survival and attained the largest sizes in the mid zones of wave-exposed and intermediately exposed areas. Since my maximum wave force meter measurements were made during relatively calm periods the differences in wave forces between the sites were relatively small. The site of intermediate wave exposure is probably similar in exposure to the wave

exposed site. In previous years while refining the maximum wave force meter design for this site, I lost equal numbers of wave meters at both the intermediate and exposed sites during stormy periods. Wave forces at these sites are also likely to depend on the swell direction. In Oregon, the summer swell is generally out of the north, while the winter swell is usually from the south. When the swell is out of the north, this site has a higher degree of wave exposure than when the swell comes from the south. The wave-protected site definitely receives far lower wave forces than either of the other two sites. I have never lost any wave force meters at the wave-protected site, or recorded forces at the maximum limit of the wave force meters, even during stormy periods.

In the northeastern Pacific, increased water motion generally results in increased productivity (Leigh et al. 1987). *Postelsia* and *Lessoniopsis* were found to be the two most productive marine plants at Tatoosh Island, a small island off the northwest coast of Washington, USA, and both of these plants are restricted to wave beaten shores (Leigh et al. 1987). Leigh et al. (1987) propose several ideas for how wave motion may enhance intertidal productivity: (1) Water motion inhibits the feeding activities of major predators and herbivore grazers in the intertidal; (2) water motion can enhance algal productivity by stripping away the boundary layer of used water from kelp blades, thereby facilitating nutrient uptake; (3) waves can continually move and exchange algal blades, thereby allowing the plant to utilize light more efficiently; and (4) wave induced disturbances can remove competitors for space.

Results of the transplant experiment suggest that the growth of *Postelsia* is somehow impaired at wave-protected sites, since plants at this

site were not competing for space and were not consumed by herbivores. Chiton densities are very low at SPDB and the most important grazers of *Postelsia* are the limpets *Lottia pelta* and *digitalis* (see Chapter IV) which are actually most abundant in the wave exposed areas. My results seem most consistent with the second (enhanced nutrient uptake by blades due to boundary layer reduction) and third (enhanced photosynthetic activity due to blade rearrangement) explanations proposed by Leigh et al. (1987) to explain the high growth rates of wave exposed *Postelsia*. As the velocity of water near a solid surface increases, the thickness of the boundary layer of slow moving water nearest to the solid surface decreases (Vogel 1981, Denny 1988). The effect of fast moving water is to essentially reduce and strip away this boundary layer, thereby providing a fresh supply of nutrients to the algal surface. Wheeler (1980) found that nutrient uptake by *Macrocystis* increases with the speed of water motion over the blades, unless the water is moving faster than 5 cm/s, at which point the rate of nutrient uptake levels off. Since 5 cm/s is an extremely low velocity for intertidal water motion, it seems unlikely that *Postelsia* growth is ever limited by reduced nutrient uptake in slow moving water. However, the *Postelsia* transplants at the wave-protected site may have experienced slow moving water conditions during calm days in summer. Koehl and Alberte (1988) propose a similar explanation to describe why *Nereocystis* found in slow moving waters have a wide, ruffled blade morphology while *Nereocystis* found in fast moving waters have thin, smooth blades. The ruffles on the blade create turbulence and effectively increase flow near the surface of the blade, thereby reducing the thickness of the boundary layer and bringing fresh nutrient filled water closer to the blade's surface. In

their experiments, the increased flux of dissolved materials to the ruffled blades' surfaces resulted in increased photosynthetic rates relative to plants with smooth blades that experienced similar flow conditions.

The stirring and continual rearrangement of new photosynthetic surfaces to light as waves strike plants is another possible explanation for the higher growth rates of plants in wave exposed versus protected areas. Holbrook et al. (1991) measured light levels under dense *Postelsia* canopies during low tides (no flow) and during moderate wave activity. They found that light flecks created as the canopy plants were rearranged by waves do not make a measurable contribution to irradiance levels in the understory. However, they suggest that the reshuffling of the blades by waves may permit different blades to emerge from the canopy at different times, thereby increasing the plant's photosynthetic opportunities. Wing and Patterson (1993) submit that the light-flash utilization efficiency of intertidal algae, such as *Postelsia* and *Hedophyllum*, at wave exposed areas may be optimal at the frequencies of wave-induced light flashes. Thus, through the interaction of reduced self-shading resulting from nearly constant movement, and enhanced light-flash utilization efficiency, these algae may have higher photosynthetic rates under a dynamic (wave exposed) light regime than under steady-state (wave protected, non-moving) light conditions.

For *Postelsia* the negative effects of living in a wave protected area were not alleviated by tidal height. Plants in the high, mid and low zones of wave protected sites all had low survival. High zone plants at all wave exposure sites had low growth rates and high mortality. Desiccation is the most likely explanation for the reduced growth of high plants. Even

naturally occurring high zone plants at wave exposed sites had stunted growth. Low zone plants also exhibited reduced growth rates and even naturally occurring low zone plants at wave exposed sites were smaller than mid zone plants. *Postelsia* does not seem to tolerate constant submergence (personal observation) and *Postelsia* are never found growing or recruiting in pools. Again, herbivory does not seem to be a likely explanation for the lack of *Postelsia* in low zone sites, since limpet grazers are actually more abundant in the mid zone and also because the low zone *Postelsia* transplants which were too large to be consumed by most herbivores, also showed reduced growth rates relative to mid zone plants.

Some intertidal plants are known to photosynthesize more efficiently in air than in water as long as they have not lost large proportions of water due to desiccation (Bidwell and Craigie 1963, Johnson et al. 1974, Quadir et al. 1979, Dring and Brown 1982, Bidwell and McLachlan 1985). Many high intertidal species such as *Fucus spiralis* (Madsen and Maberly 1990), *Fucus distichus* (Johnson et al. 1974, Quadir et al. 1979), *Hesperophycus harveyanus, Pelvetia fastifiata* f. *gracilis* (Oates and Murray 1983), *Endocladia muricata, Porphyra perorata* and *Iridaea flaccida* (Johnson et al. 1974) are photosynthetically stimulated by slight desiccation. The alternating exposure to air may actually be beneficial by increasing the daily carbon gain compared to a fully submerged situation (Sand-Jensen and Gordon 1984, Holbrook et al. 1988). Although the photosynthetic performance of *Postelsia* in air and water have not been measured, this seems to be a likely explanation for their restriction to mid zone sites. The deeply grooved morphology of *Postelsia* blades may allow

these surfaces to hold water and prevent desiccation at mid zone sites. Further studies on the photosynthetic performance of *Postelsia* in air and water and at different flow levels would provide a useful link to understanding the factors that limit the growth of *Postelsia* in wave protected areas and at high and low zone sites.

CONCLUSION

The annual life history of *Postelsia* seems ideally suited to life in a seasonally disturbed environment. Areas of mussel beds that are disturbed by wave action in the winter have the highest recruitment of *Postelsia* in the following spring, presumably because the sea palm propagules can survive beneath the mussel bed in fall and are somehow stimulated to germinate by the occurrence of a winter disturbance. Although the dispersal of sea palm spores is limited in distance, there may be some secondary short distance dispersal at the gamete stage or via mobile animals. *Postelsia* seem to be restricted to wave exposed areas due to optimal physical conditions at these sites that enhance growth, and are not able to survive and grow in wave protected areas, even in the absence of competition for space. Zonation of sea palms with respect to tidal height seems to be controlled by the preference of *Postelsia* for physiological conditions provided by intermittent exposure to air and constant stirring of blades and splashing present at mid zone wave exposed sites.

TABLES

Table III.1.

Repeated measures ANOVA of the effect of disturbance regime (treatment) and sampling date on *Postelsia* density (log transformed) in the year following the experimental manipulations.

1992

	df	MS	F-Ratio	p
Between Subjects				
Treatment	3	3.915	0.844	0.496
Error	12	4.640		
Within Subjects				
Date	3	1.784	5.339	0.004
Treatment x Date	9	0.464	1.388	0.230
Error	36	0.334		

MULTIVARIATE REPEATED MEASURES ANALYSIS

	df	Wilks' Lamba	F-Ratio	p
Date	3, 10	0.380	5.443	0.018
Treatment x Date	9, 24	0.374	1.354	0.262

1993

	df	MS	F-Ratio	p
Between Subjects				
Treatment	3	64.946	32.990	<0.001
Error	12	1.969		
Within Subjects				
Date	6	0.943	8.077	<0.001
Treatment x Date	18	0.234	2.005	0.020
Error	72	0.117		

MULTIVARIATE REPEATED MEASURES ANALYSIS

	df	Wilks' Lamba	F-Ratio	p
Date	6, 7	0.178	5.402	0.022
Treatment x Date	18, 20	0.072	1.725	0.118

Table III.2.

Repeated measures ANOVA of the effect of disturbance regime (treatment) and sampling date on *Postelsia* density (log transformed) in both the 1991 and 1992 winter and summer disturbance plots in 1993.

	df	MS	F-Ratio	p
Between Subjects				
Treatment	3	17.123	2.919	0.078
Error	12	5.866		
Within Subjects				
Date	6	1.403	9.166	<0.001
Treatment x Date	18	0.096	0.626	0.868
Error	72	0.153		

MULTIVARIATE REPEATED MEASURES ANALYSIS

	df	Wilks' Lamba	F-Ratio	p
Date	6, 7	0.222	4.078	0.044
Treatment x Date	18, 20	0.431	0.390	0.975

Table III.3.

Density of *Postelsia* per 0.25 m^2 plot in the *Postelsia* seeding experiment at FCP.

Treatment	Plot	March	May	June	July	August	October
Summer	1	12	9	10	10	8	1
Disturbance	2	0	0	0	0	0	0
	3	6	2	2	4	2	1
	4	0	6	0	0	0	0
Winter	1	0	5	1	1	1	0
Disturbance	2	0	0	0	0	0	0
	3	24	38	35	30	25	5
	4	0	0	0	0	0	0
Winter	1	0	0	0	0	0	0
Disturbance +	2	0	1	0	0	0	0
Sterilization	3	0	0	0	0	0	0
	4	0	0	0	0	0	0
Unmanipulated	1	0	60	52	38	30	5
Control	2	0	0	0	0	0	0
	3	0	2	0	0	0	0
	4	0	1	27	10	0	0

Table III.4.

Repeated measures ANOVA of the effect of wave meter location (site) and sampling date on maximum wave forces (log transformed) at SPDB in 1993.

	df	MS	F-Ratio	p
Between Subjects				
Site	2	1.154	10.206	0.017
Error	5	0.113		
Within Subjects				
Date	5	0.167	3.069	0.027
Site x Date	10	0.057	1.052	0.432
Error	25	0.054		

MULTIVARIATE REPEATED MEASURES ANALYSIS

	df	Wilks' Lamba	F-Ratio	p
Date	5, 1	0.067	2.768	0.426
Site x Date	10, 2	0.013	1.569	0.451

Table III.5.

Comparison of proportional survival and expected mortality of *Postelsia* transplants in (a) the low zone; (b) the mid zone; (c) the high zone; (d) the protected site; (e) the intermediate site; and (f) the exposed site. Short term logrank statistics (LR) between consecutive census dates are shown. $d1_i$ = number of deaths in group 1 at time interval i. $d2_i$ = number of deaths in group 2 at time interval i. $d3_i$ = number of deaths in group 3 at time interval i. $E1_i$ = expected number of deaths in group 1 in interval i. $E2_i$ = expected number of deaths in group 2 in interval i. $E3_i$ = expected number of deaths in group 3 in interval i. LR = Logrank statistic comparing mortality risks among groups in time interval i and over the sampling period.

$$LR = [(d_1 - E_1)^2/E_1 + (d_2 - E_2)^2/E_2 + (d_3 - E_3)^2/E_3]$$

Logrank statistic is compared to a chi-squared distribution. ** = $p < 0.01$; * = $p<0.05$; NS = not significant.

a)

i	*d1i*	*d2i*	*d3i*	*E1*	*E2i*	*E31*	LR	p
1	2	1	1	1.5	1.5	1.5	0.5	NS
2	8	4	2	5.7	6.4	6.4	4.8	NS
3	0	0	0	0	0	0	-	-
4	0	1	2	0	1	0.8	-	-
5	0	1	1	0	1	0.5	-	-
6	0	1	0	0	1	0.3	-	-
7	0	1	1	0	1	0.5	-	-
8	0	1	0	0	1	0	-	-
ALL	10	10	10	7.9	7.9	7.9	2.3	NS

(b)

i	*d1i*	*d2i*	*d3i*	*E1*	*E2i*	*E31*	LR	p
1	2	7	4	4.5	4.5	4.5	2.8	NS
2	0	0	0	0	0	0	-	-
3	7	0	2	5.1	1.9	3.8	3.5	NS
4	1	0	0	0.3	0.8	1	4	NS
5	0	0	1	0	0	0	-	-
6	0	0	1	0	0	0	-	-
7	0	3	1	0	3	2	-	-
ALL	10	10	10	9.6	6.4	8.3	2.4	NS

Table III.5 (Continued)

(c)

i	d_{1i}	d_{2i}	d_{3i}	E_1	E_{2i}	E_{31}	LR	p
1	6	6	4	6	6	6	0.7	NS
2	2	0	1	1	1	1.5	2.2	NS
3	2	3	3	1.7	3.3	4.2	0.4	NS
4	0	1	2	0	1	2	-	-
ALL	10	10	10	8.7	10.3	11.7	0.5	NS

(d)

i	d_{1i}	d_{2i}	d_{3i}	E_1	E_{2i}	E_{31}	LR	p
1	2	2	6	2	2	2	8	*
2	8	0	2	4	4	2	8	*
3	0	7	2	0	7	1.8	-	-
4	0	1	0	0	1	0	-	-
ALL	10	10	10	6	13	5.8	6.5	*

(e)

i	d_{1i}	d_{2i}	d_{3i}	E_1	E_{2i}	E_{31}	LR	p
1	1	7	6	4	4	4	5.5	NS
2	4	0	0	3	1	1.3	2.7	NS
3	0	0	3	0	0	0	-	-
4	1	0	1	0.6	0.4	0.1	6.7	*
5	1	0	0	0.6	0.4	0	-	-
6	1	0	0	0.5	0.5	0	-	-
7	1	3	0	1.6	2.4	0	-	-
8	1	0	0	1	0	0	-	-
ALL	10	10	10	7	5	5.3	104	**

(f)

i	d_{1i}	d_{2i}	d_{3i}	E_1	E_{2i}	E_{31}	LR	p
1	1	4	4	2.5	2.5	2.5	2.7	NS
2	2	0	1	1.2	0.8	0.8	1.4	NS
3	3	2	3	2.7	2.3	1.9	0.7	NS
4	2	0	2	1	1	0.5	6.5	*
5	1	1	0	0.7	1.3	0	-	-
6	0	1	0	0.3	0.8	0	-	-
7	1	1	0	0.7	1.3	0	-	-
8	0	1	0	0	1	0	-	-
ALL	10	10	10	6.4	5.6	5.2	9.9	**

Table III.6.

Repeated measures ANOVA of the effect of tidal height (height), wave exposure (exposure) and sampling date on log transformed *Postelsia* (a) stipe length; (b) basal stipe width; and (c) total blade surface area in April and May 1993.

(a) STIPE LENGTH

	df	MS	F-Ratio	p
Between Subjects				
Height	3	0.893	9.153	<0.001
Exposure	2	0.333	3.417	0.041
Height x Exposure	4	0.120	1.234	0.309
Error	48	0.098		
Within Subjects				
Date	1	4.917	267.741	<0.001
Height x Date	2	0.319	17.379	<0.001
Exposure x Date	2	0.107	5.847	0.005
Height x Exposure x Date	4	0.010	0.566	0.688
Error	48	0.018		

(b) STIPE WIDTH

	df	MS	F-Ratio	p
Between Subjects				
Height	2	0.307	5.080	0.010
Exposure	2	0.040	0.668	0.517
Height x Exposure	4	0.226	3.735	0.010
Error	48	0.060		
Within Subjects				
Date	1	3.121	274.677	<0.001
Height x Date	2	0.126	11.055	<0.001
Exposure x Date	2	0.071	6.275	0.004
Height x Exposure x Date	4	0.011	1.005	0.414
Error	48	0.011		

Table III.6 (Continued)

(c) TOTAL BLADE SURFACE AREA

	df	MS	F-Ratio	p
Between Subjects				
Height	2	0.163	1.118	0.337
Exposure	2	0.029	0.199	0.820
Height x Exposure	4	0.249	1.712	0.166
Error	41	0.146		
Within Subjects				
Date	1	20.228	335.155	<0.001
Height x Date	2	0.379	6.272	0.004
Exposure x Date	2	0.152	2.521	0.093
Height x Exposure x Date	4	0.185	3.065	0.027
Error	41	0.060		

Table III.7.

Two-way ANOVA of the effect of plant type (natural or transplant) and tidal height (height) on log transformed (a) stipe length, (b) basal stipe width, and (c) total blade surface area from natural *Postelsia* and *Postelsia* transplants at SPDB in August 1993 (high transplants are from July, since there were none remaining in August). Tidal height and plant type were considered fixed and sums of squares are type III.

(a) STIPE LENGTH

	df	MS	F-Ratio	p
Plant type	1	0.253	4.529	0.042
Height	2	5.379	96.236	<0.001
Plant type x Height	2	0.534	9.552	0.001
Error	30	0.056		

(b) STIPE WIDTH

	df	MS	F-Ratio	p
Plant type	1	0.433	17.449	<0.001
Height	2	2.089	84.082	<0.001
Plant type x Height	2	0.050	1.995	0.154
Error	30	0.025		

(c) TOTAL BLADE SURFACE AREA

	df	MS	F-Ratio	p
Plant type	1	0.291	1.141	0.293
Height	2	13.510	53.019	<0.001
Plant type x Height	2	0.119	0.466	0.632
Error	32	0.255		

FIGURES

Figure III.1. Annual life history of *Postelsia palmaeformis*. Macroscopic adult sporophytes become reproductive and release microscopic spores in mid-summer. Spores germinate into microscopic gametophytes which sexually reproduce and form the sprorophyte stage sometime between fall and spring. Young sporophytes are usually visible in late winter/early spring.

Figure III.1

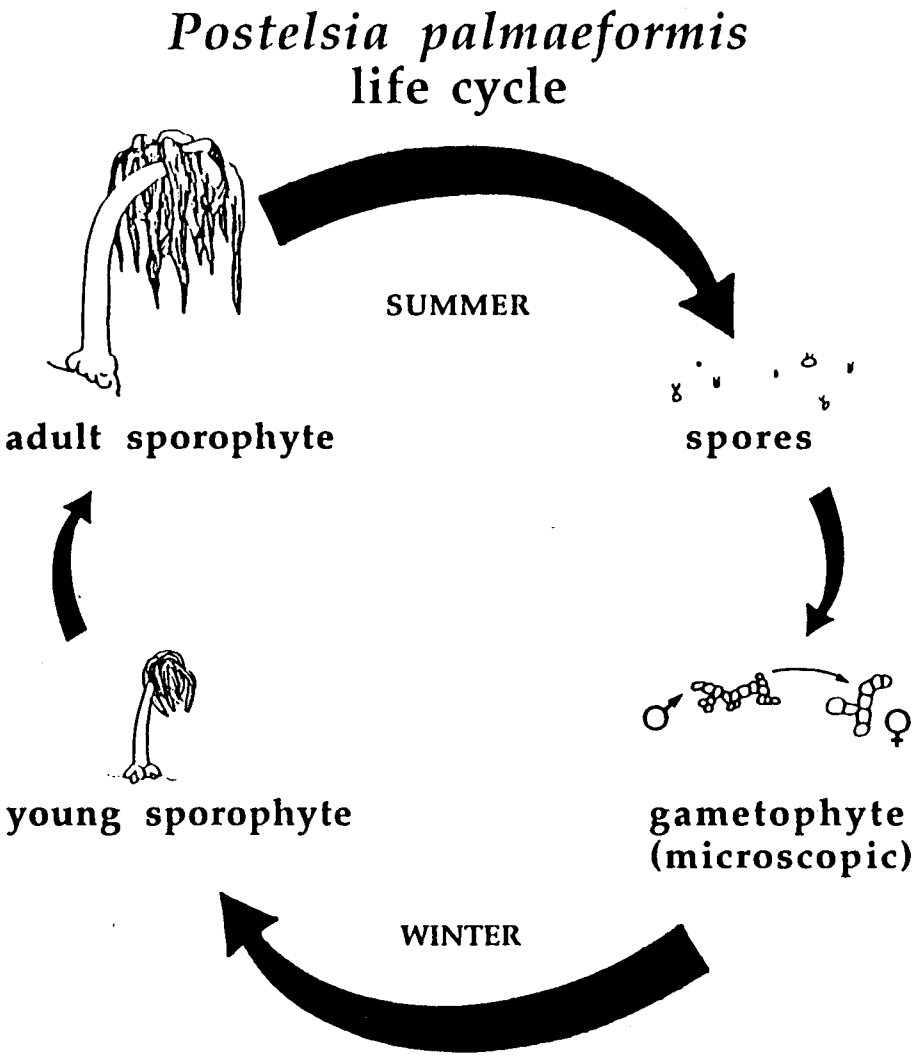

Postelsia palmaeformis
life cycle
SUMMER
adult sporophyte
spores
young sporophyte
gametophyte
(microscopic)
WINTER

Figure III.2. Experimental mussel disturbance sampling design. 1 = summer mussel removal, 2 = winter mussel removal, 3 = winter mussel removal plus sterilization. Treatment 1 plots were censused monthly following the disturbance, although no *Postelsia* were present until the following spring. All plots were censused monthly in the following spring, summer and fall.

Figure III.2

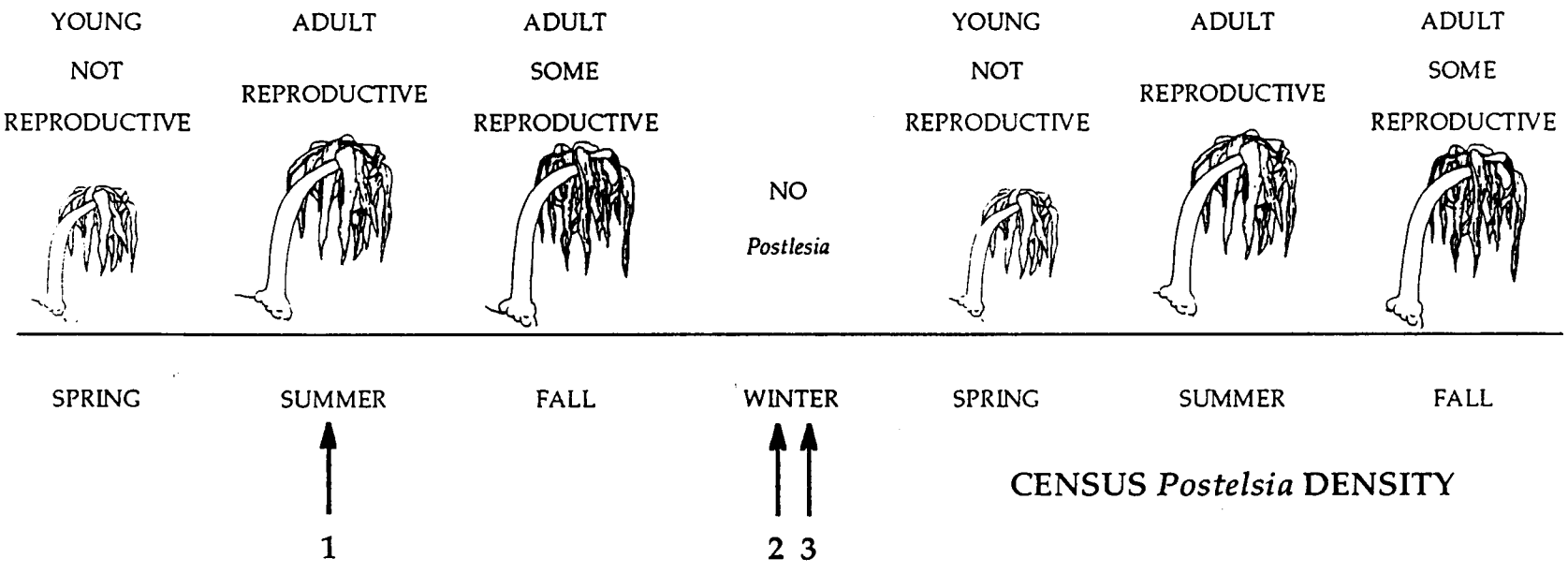

YOUNG
NOT
REPRODUCTIVE
ADULT
REPRODUCTIVE
ADULT
SOME
REPRODUCTIVE
NO
Postlesia
YOUNG
NOT
REPRODUCTIVE
ADULT
REPRODUCTIVE
ADULT
SOME
REPRODUCTIVE
SPRING
SUMMER
FALL
WINTER
SPRING
SUMMER
FALL
1
2 3
CENSUS Postelsia DENSITY

Figure III.3. Wire baskets used for the *Postelsia* seeding experiment at FCP. Each basket was filled with the bladed portions from ten reproductively mature *Postelsia* and strapped down over each plot in mid-summer.

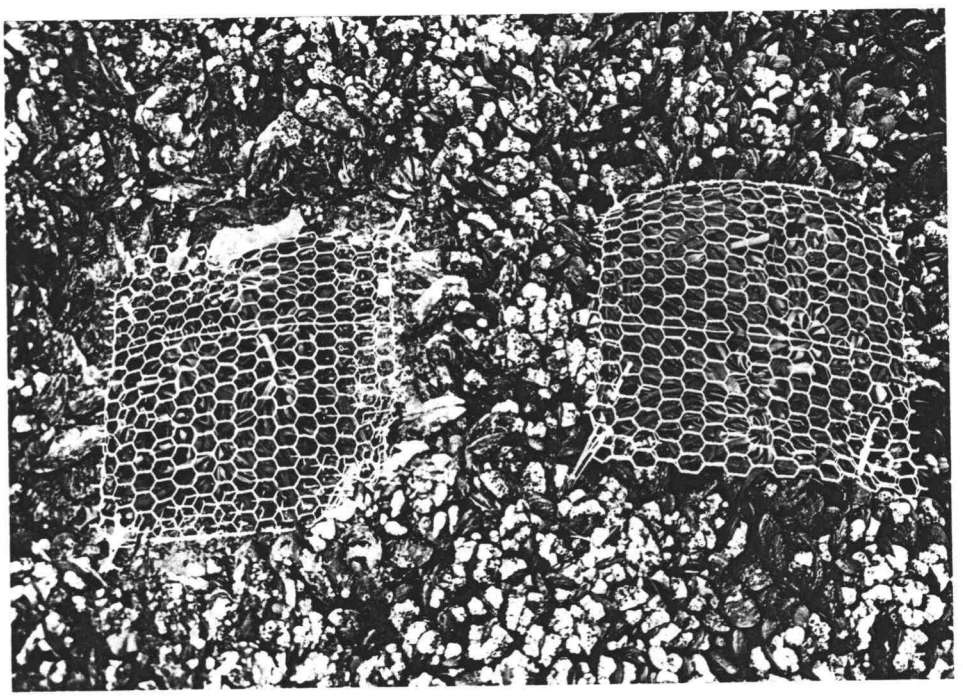


Figure III.4. A representative *Postelsia* transplant. The marine epoxy putty is used to secure the mussel in the rock hole. The sea palm holdfasts overgrow the mussel and putty within one to two months following the transplant procedure.

Figure III.5. Mean density of *Postelsia* (± 1 s.e.m.) in each of the treatment plots in the first year (1992) of the mussel removal experiment.

Figure III.5

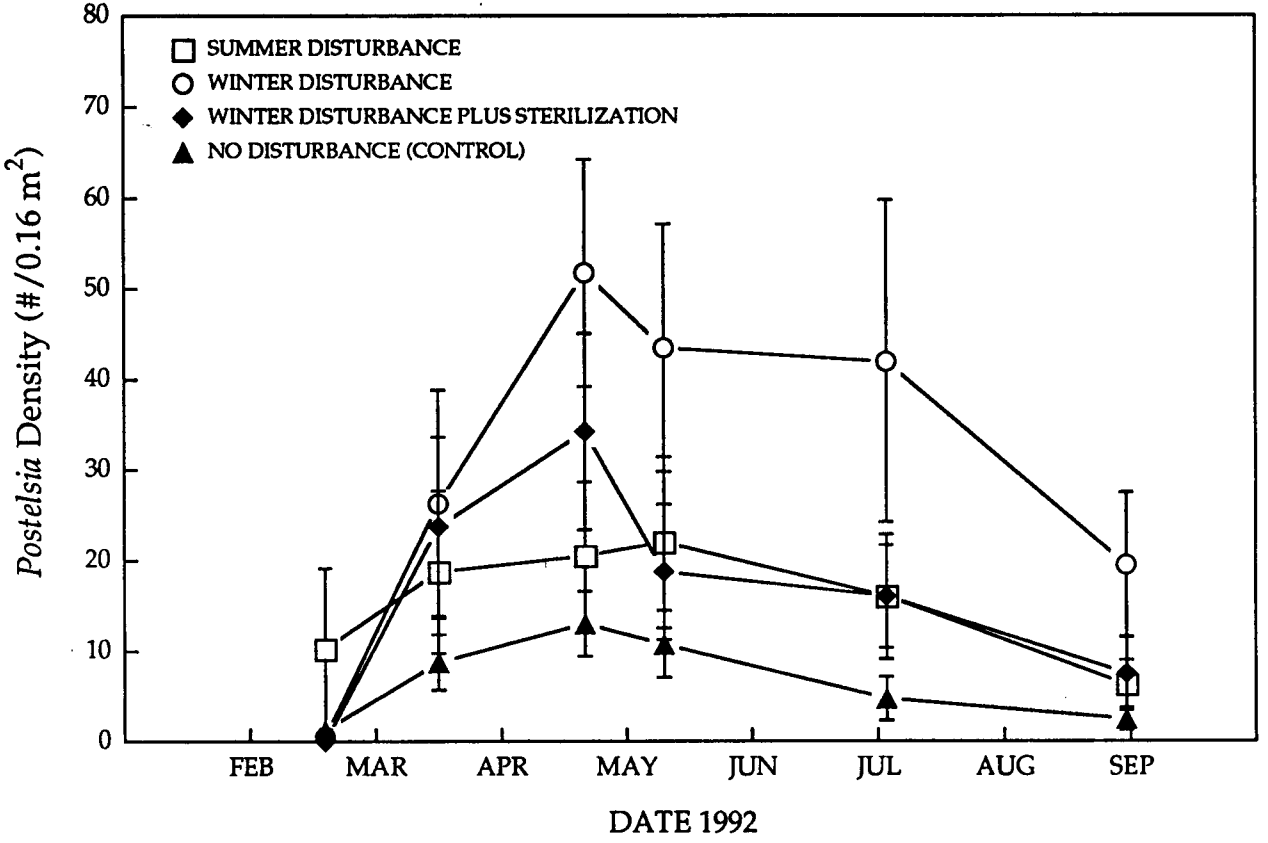
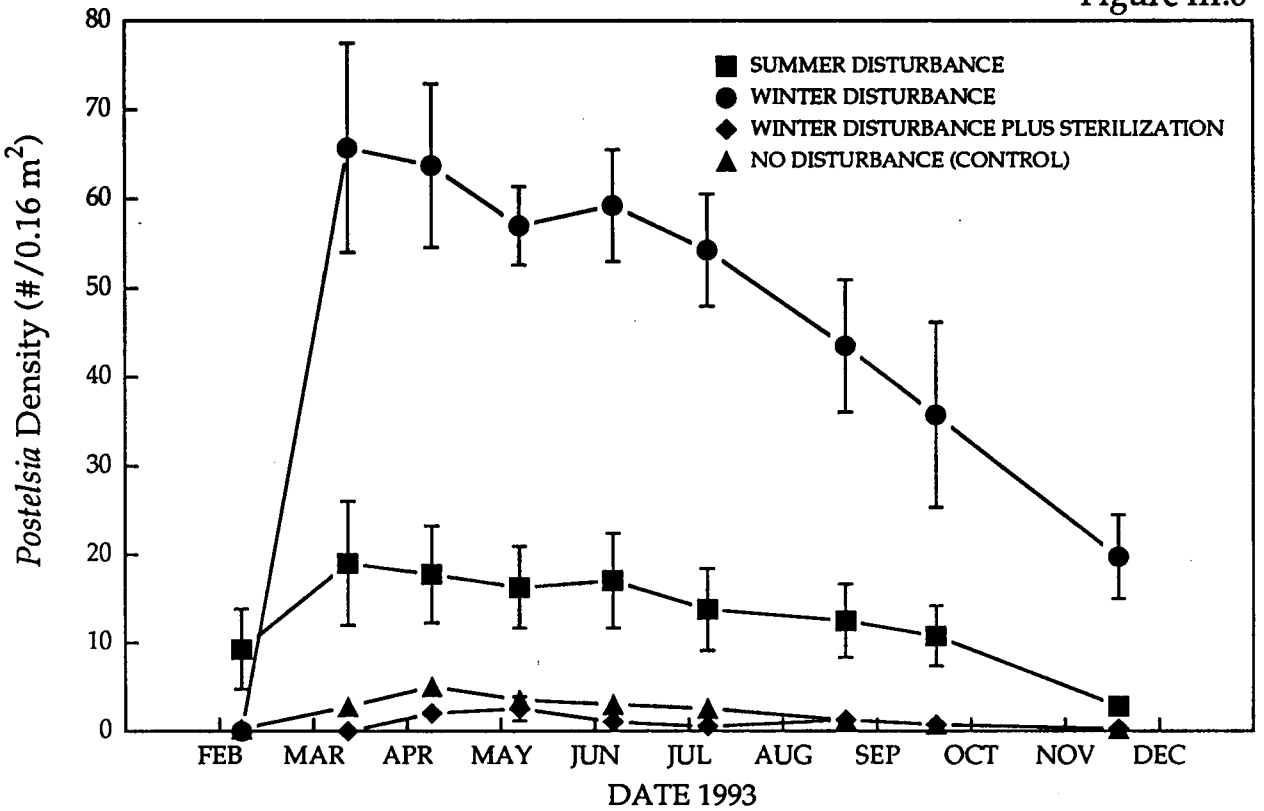

SUMMER DISTURBANCE
WINTER DISTURBANCE
WINTER DISTURBANCE PLUS STERILIZATION
NO DISTURBANCE (CONTROL)
Postelsia Density (#/0.16 m2)
80
70
60
50
40
30
20
10
0
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
DATE 1992

Figure III.6. Mean density of *Postelsia* (± 1 s.e.m.) in each of the treatment plots in the second year (1993) of the mussel removal experiment. Multiple comparisons based on a repeated measures analysis of variance were done within each month from March to September when *Postelsia* were at peak densities. *= significance at $p<0.05$, **= significance at $p<0.01$.

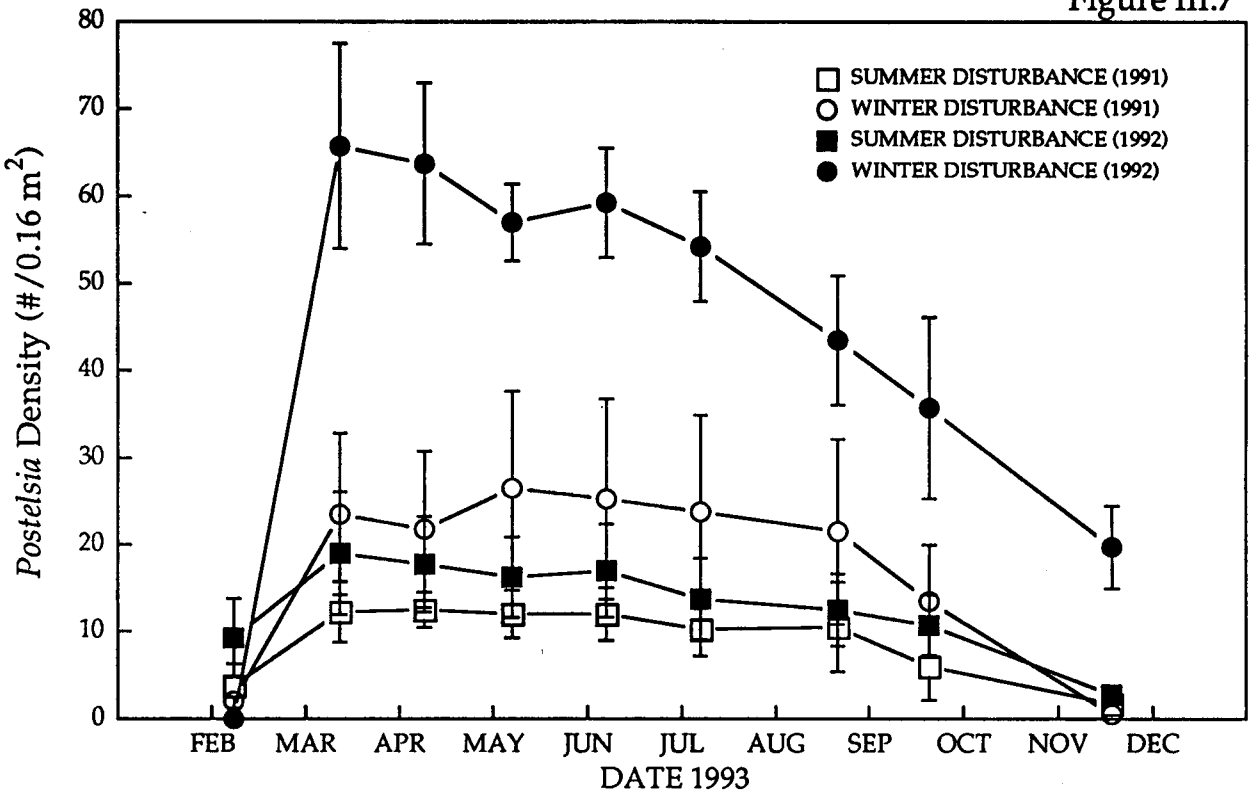
Figure III.6



EFFECT OF:	MAR	APR	MAY	JUN	JUL	AUG	SEP
CLEARING WINTER (● VS ▲)	**	**	**	**	**	**	**
CLEARING SUMMER (■ VS ▲)	**	NS	*	**	**	**	**
SCRAPING (◆ VS ●)	**	**	**	**	**	**	**
CLEARING AND SCRAPING (◆ VS ▲)	*	NS	NS	NS	*	NS	NS

Figure III.7. Mean densities of *Postelsia* (± 1 s.e.m.) in 1993 in both the winter and summer mussel removal treatments from disturbances initiated in the first year (1991, represented as open symbols) and the second year (1992, represented as closed symbols).

Figure III.7



EFFECT OF:	MAR	APR	MAY	JUN	JUL	AUG	SEP
BETWEEN YEARS (WINTER) (○ VS ●)	NS	*	*	*	*	NS	NS
BETWEEN YEARS (SUMMER) (□ VS ■)	NS	NS	NS	NS	NS	NS	NS
SEASON WITHIN YEARS (1991) (○ VS □)	NS	NS	NS	NS	NS	NS	NS
SEASON WITHIN YEARS (1992) (● VS ■)	*	*	**	*	*	**	NS

Figure III.8. Mean maximum wave forces (± 1 s.e.m.) (log transformed) recorded by maximum wave force meters at the wave protected, intermediate, and exposed sites at SPDB.

Figure III.8

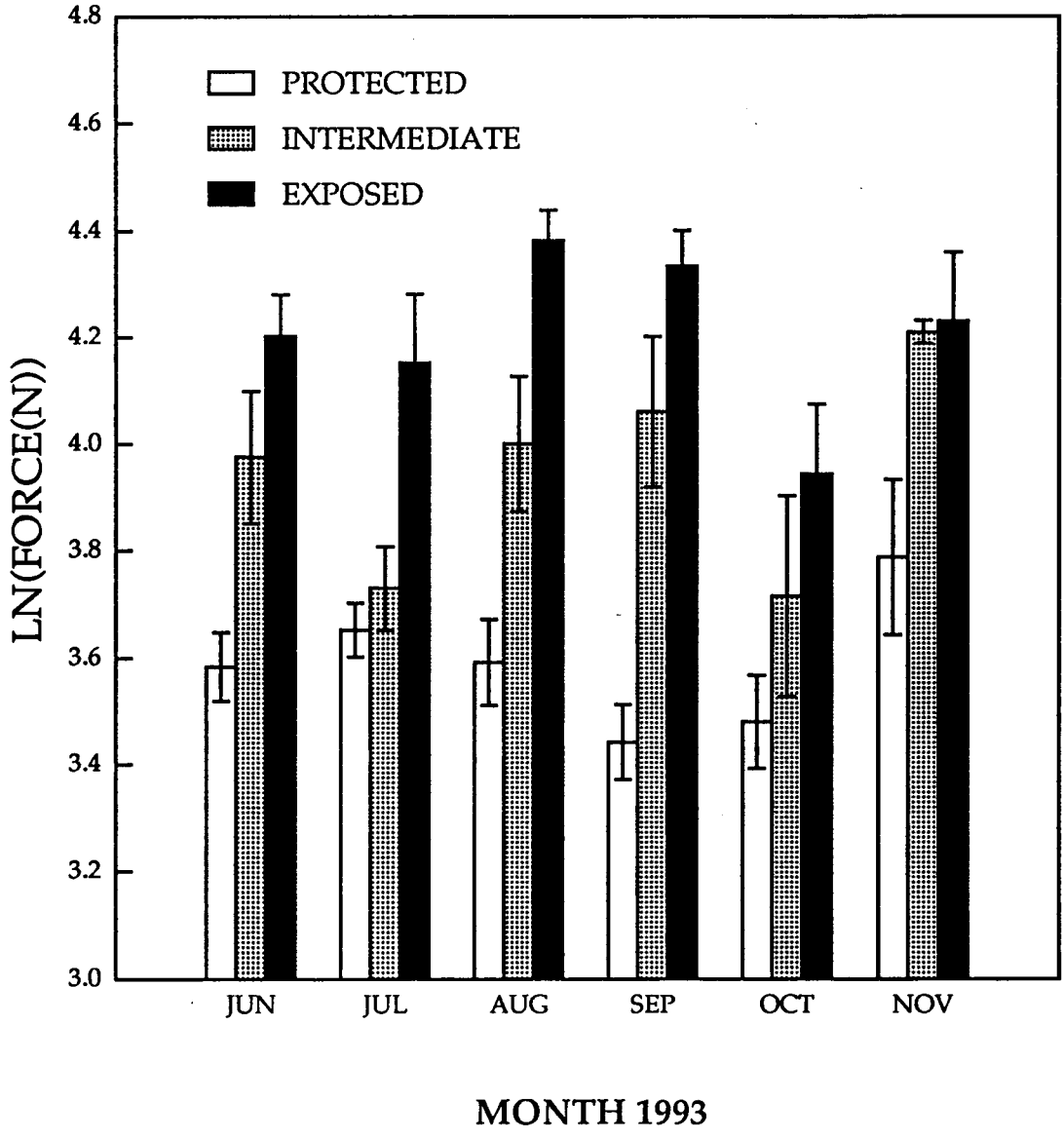

4.8
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
LN(FORCE(N))
PROTECTED
INTERMEDIATE
EXPOSED
JUN
JUL
AUG
SEP
OCT
NOV
MONTH 1993

Figure III.9. Absolute number of *Postelsia* present in each of the transplant treatment groups at SPDB each month in the summer of 1993.

Figure III.9

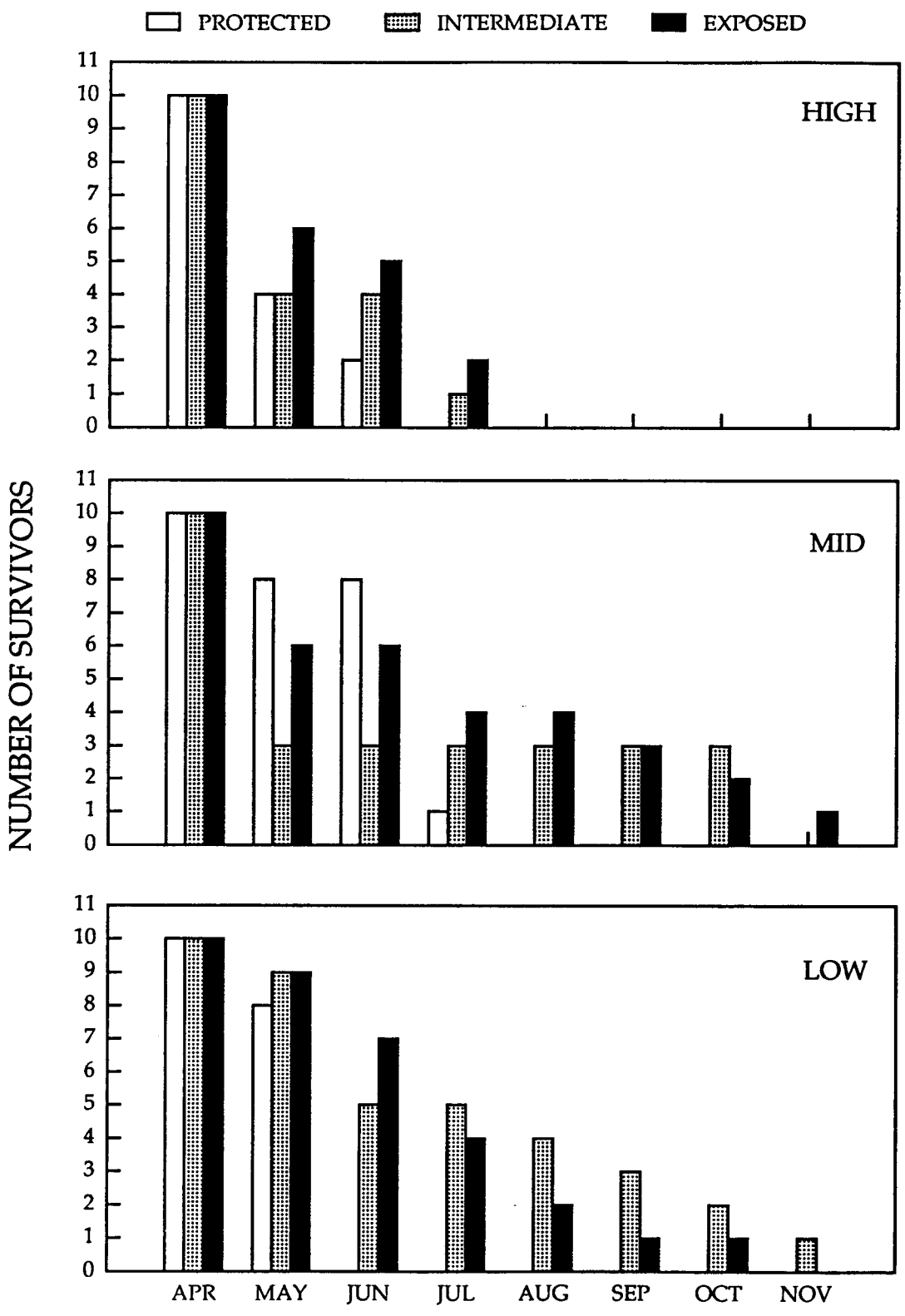

PROTECTED
INTERMEDIATE
EXPOSED
HIGH
MID
LOW
NUMBER OF SURVIVORS
0
1
2
3
4
5
6
7
8
9
10
11
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV

Figure III.10. Mean stipe lengths (± 1 s.e.m.) of *Postelsia* in each of the transplant treatment groups at SPDB each month in the summer of 1993.

Figure III.10

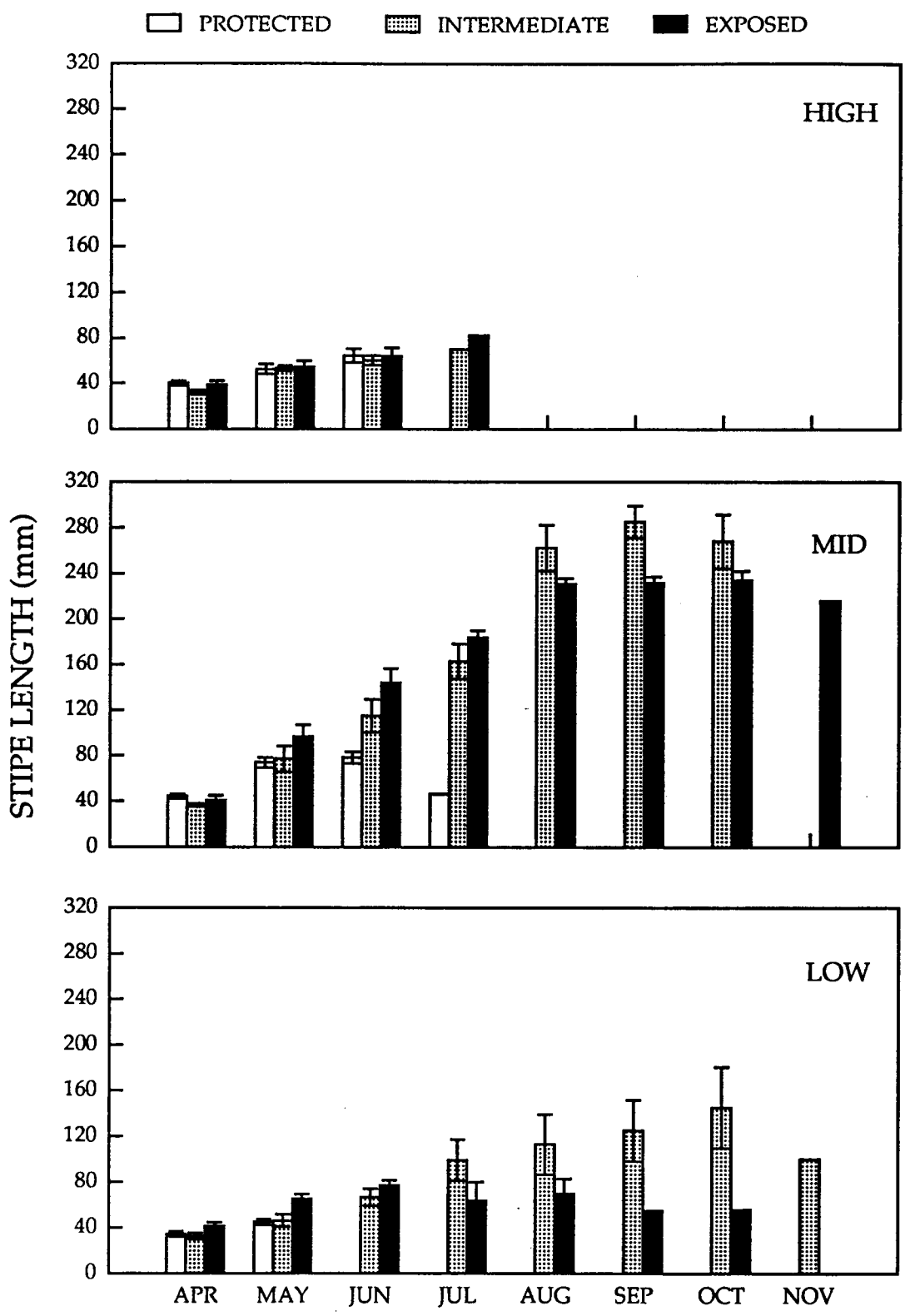


Figure III.11. Mean basal stipe width (± 1 s.e.m.) (measured just above the holdfast) of *Postelsia* in each of the transplant treatment groups at SPDB each month in the summer of 1993.

Figure III.11

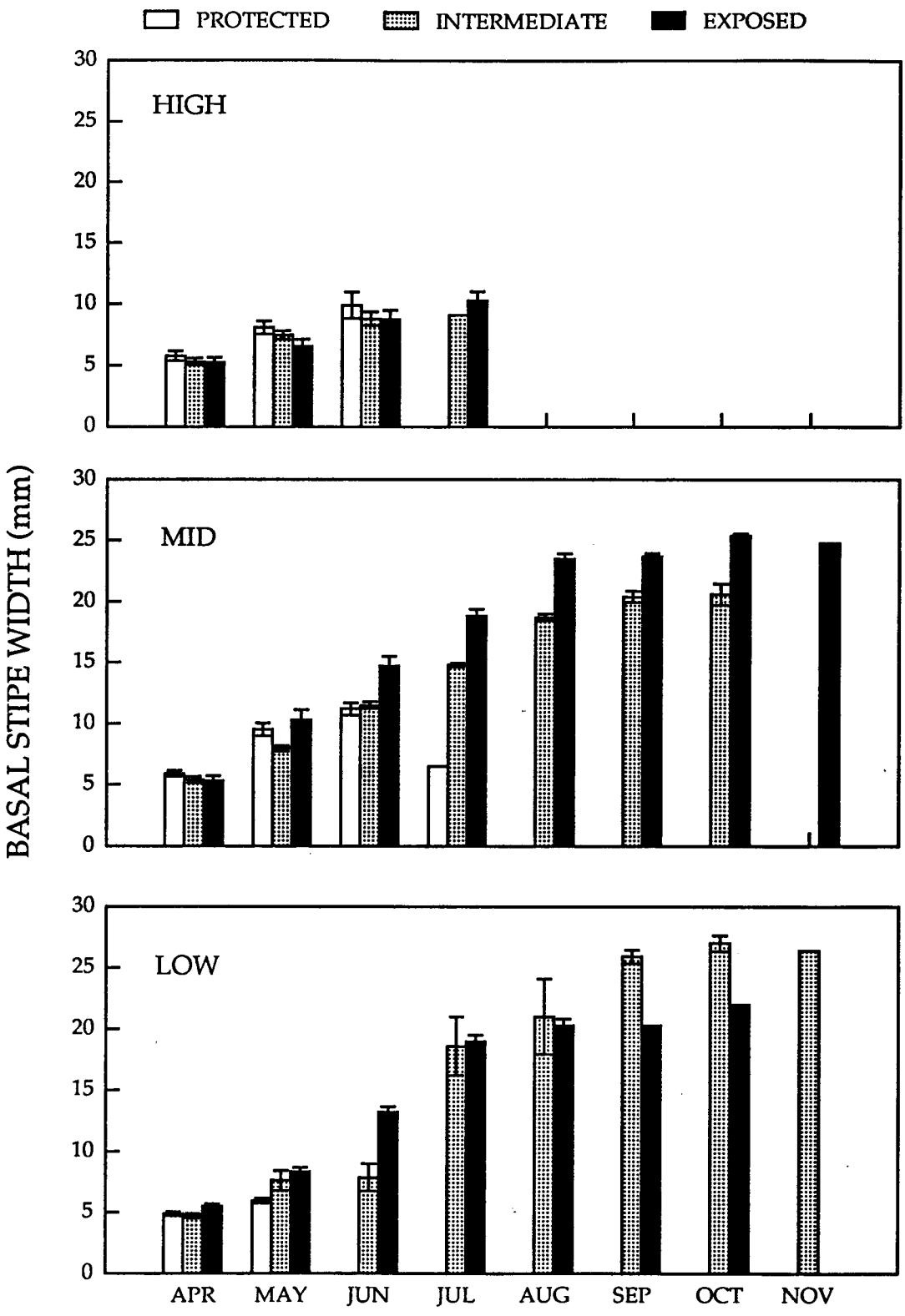


Figure III.12. Mean total blade surface areas per plant (± 1 s.e.m.) in each of the transplant treatment groups at SPDB each month in the summer of 1993.

Figure III.12

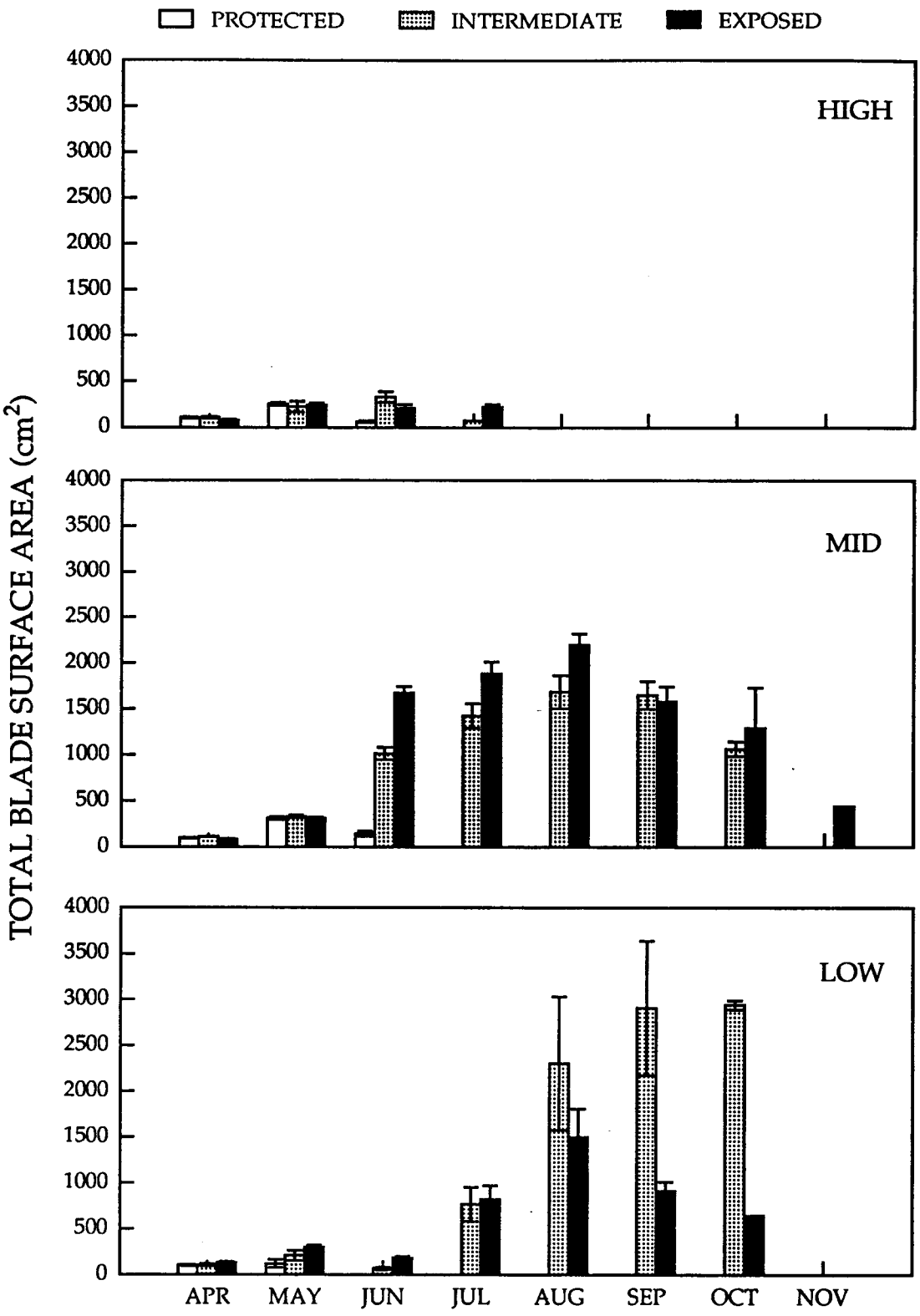
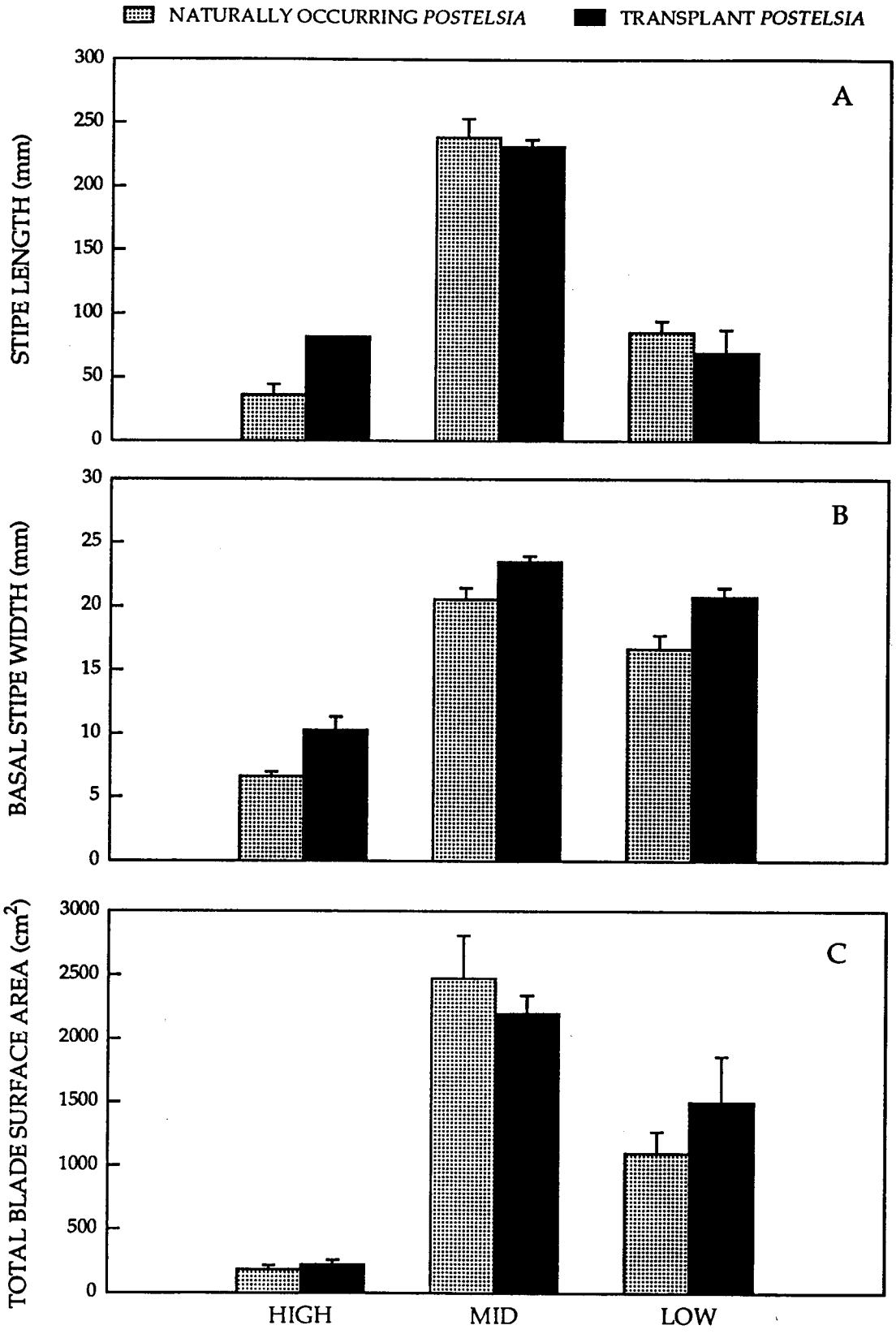


Figure III.13. Mean measurements: (a) stipe length (mm), (b) basal stipe width (mm) and (c) total blade surface area (cm^2) all ± 1 s.e.m. from wave exposed *Postelsia* transplants and naturally occurring *Postelsia* at the wave exposed site in August 1993 (except high zone transplants measured in July 1993) taken from the high zone (above the main *Postelsia* zone), mid zone (chosen from the middle of the *Postelsia* zone) and low zone (below the main *Postelsia* zone). N=10 for all naturally occurring plants, N=2 for high and low zone transplants, and N=4 for mid zone transplants.

Figure III.13



Chapter IV

THE RELATIVE IMPORTANCES OF COMPETITION, DISTURBANCE AND PREDATION IN A ROCKY INTERTIDAL, "KELP FOREST" COMMUNITY

ABSTRACT

The sea palm, *Postelsia palmaeformis* is a conspicuous member of highly wave exposed, rocky intertidal communities along the northeastern Pacific coast. It is an annual brown alga and because of its large, tree-like morphology, areas with this plant resemble intertidal kelp forests. *Postelsia* forms large continuous beds in two types of habitat: in horizontal or slightly sloping mussel-dominated areas and in steeply sloping rocky areas, with an understory community composed mostly of "turfy" red algal species.

I experimentally examined the importances of competition (for space and light), disturbance and predation in structuring the *Postelsia* understory community on steep, rocky slopes. I conducted controlled and replicated experiments over a two year period in which I: 1) completely removed *Postelsia* from experimental areas; 2) reduced *Postelsia* densities; 3) removed blades from *Postelsia* and 4) removed limpet grazers. In a third year, I ceased maintaining the manipulations to determine the rates of recovery of *Postelsia* and the understory community.

Removal of *Postelsia* from this community led to significant increases in the abundances of two common understory species, *Corallina vancouveriensis* and *Microcladia borealis*. Both removal of *Postelsia* and

thinning of *Postelsia* densities resulted in higher species diversities in the algal understory community than in the unmanipulated plots. Plots that were not shaded by a *Postelsia* canopy also had higher species diversity in the understory community than unmanipulated plots. *Hymenena* sp. was the only understory alga to decrease in the absence of shade. Abundances of *Postelsia* in all treatments were "unusually" low in the recovery period, however *Postelsia* densities in plots that had previously been thinned were significantly higher than those of unmanipulated plots in the final spring. Grazing by limpets had a large negative effect on *Postelsia*. Treatments without limpets had significantly higher densities and percent covers of *Postelsia*, and *Postelsia* were taller in the more densely aggregated plots. Removal of limpets also led to a decrease in the species diversity of the algal understory community.

Competition, disturbance and grazing were all important factors in structuring this community. *Postelsia* were dominant competitors and their holdfasts overgrew low-lying plants which were torn loose with *Postelsia* when this kelp was dislodged by winter storm surf. In the absence of this predictable, seasonal disturbance, competitive understory species, such as *Corallina* dominated primary space. Intermediate levels of disturbance (in the thinned *Postelsia* density treatments) allowed for the highest understory diversity. Preferential grazing of *Postelsia* by limpets regulated the abundance of *Postelsia* and also helped maintain high levels of diversity in the algal understory. Limpets had positive indirect effects on understory algal species through removal of *Postelsia*, which was the competitive dominant during most of the year. In the natural system, both disturbance and predation are important factors in maintaining high levels

of diversity in the understory community, providing opportunities for other less competitive species to settle and grow. Disturbances created by *Postelsia* dislodgment prevent the monopolization of space by fast-growing, turfy understory species, and limpet grazers play a keystone role by regulating densities of *Postelsia*.

INTRODUCTION

One of the major goals of community ecology is to understand the causes and patterns of species diversity and community structure. Patterns of diversity in some cases result from complex interactions between biotic and abiotic factors. The structure of the community is dependent on the physical nature of the environment (temperature, salinity, nutrient and light availability, wave exposure) and interactions between organisms in the community (competition, predation, recruitment, mutualism, and indirect effects of these factors) (Menge and Farrell 1989).

The effects of competition, predation and disturbance have been well studied in marine systems. In many ecological communities, particularly those of the marine rocky-intertidal, space is the primary limiting resource and competition for space may eliminate all but one or a few competitive dominant species (Connell 1961, Paine 1966, 1974, Dayton, 1971, Menge 1976, Lubchenco and Menge 1978, Paine and Levin 1981). Competition for light plays an important role in structuring terrestrial plant communities (Harper 1977) and subtidal algal communities (Dayton 1975, Reed and Foster 1984, Kennelly 1987c, 1989). Disturbances can renew bare rock space and indirectly alter competitive interactions. In marine systems disturbances are often caused by high water motion which can dislodge organisms from the rock (Dayton 1971, Sousa 1979, Pickett and White 1985, Ebling et al. 1985, Kennelly 1987, Paine 1988). Environments that are subject to intermediate levels of disturbance often have high species diversities, since disturbances can renew space, the primary limiting resource and initiate the successional sequence of species

replacement (Dayton 1971, Connell 1978, Sousa 1979). Predation can also have strong effects on community structure. Certain keystone species can play a role analogous to that of physical disturbance by selectively preying on competitive dominants, thereby allowing other less-competitive species to invade the space vacated by the competitive dominant. In addition, grazers may indirectly alter competitive interactions by regulating algal abundances (Paine and Vadas 1969, Vadas 1969, Estes et al. 1978, Lubchenco 1978, Lubchenco and Menge 1978, Pearse and Hines 1979, Duggins 1980, Hixon and Brostoff 1983). Differences in the relative importances of disturbance, competition and predation in structuring communities are likely to vary over space and time (Menge and Sutherland 1987), and are likely to vary seasonally in communities which are subject to regular, seasonal disturbances and which contain species with annual life histories.

The marine, rocky intertidal zone of the Pacific Northwest has served as a model system for studies of community ecology and is an ideal system for ecological experimental manipulations due to the high diversity of sessile species on a relatively small spatial scale. The middle intertidal zones of wave-swept rocky shores along the northeastern Pacific are dominated by the mussel *Mytilus californianus*, a competitively dominant bivalve that often forms thick and long-lasting beds. Seasonal wave disturbances remove patches of *Mytilus*, thus creating bare spaces onto which other species recruit. In this manner, storms maintain higher levels of diversity than would otherwise occur (Paine and Levin 1981). Biotic factors also affect diversity. The seastar *Pisaster* is a keystone predator in this system which selectively feeds on *Mytilus*, thereby also helping to maintain a high level of diversity (Paine 1974). Competition, disturbance

and predation all play important roles in structuring the middle-intertidal zone.

At extremely wave exposed sites from Vancouver Island, B. C. to central California, the sea palm, *Postelsia palmaeformis* can be found as a conspicuous member of the middle intertidal flora (Dayton 1973, Abbott and Hollenberg 1976, Paine 1979, 1988). *Postelsia* is an annual brown alga (kelp) which can grow to a height of 0.75 m in late summer, but is absent from the community each winter when mature plants senesce and are torn from the substratum by winter storm surf. *Postelsia* can overgrow and remove mussels when it is torn from the rock in winter, but *Postelsia* remains a subordinate competitor to *Mytilus*, which eventually fill in spaces occupied by *Postelsia* (Paine 1979). *Postelsia*, therefore, appears to require the frequent disturbance of wave forces to remove mussels and renew primary space, and is not found in wave-protected areas, where it may be outcompeted by *Mytilus* (Paine 1979).

All of the published studies of *Postelsia*'s ecology have examined plants growing in horizontal or slightly sloping mussel-dominated areas. *Postelsia* that grow on vertical or near-vertical slopes tend to be found at higher tidal elevations (usually above the *Mytilus* dominated zone), and in association with an understory community composed of various species of mostly red, turfy algae (personal observation). *Postelsia* in these vertically-sloping areas are not in direct competition with *Mytilus*, and form extensive beds (not patches, as they do in *Mytilus* dominated areas). In the summer, *Postelsia* seem to be the dominant competitors on vertical slopes, and their holdfasts rapidly overgrow low-lying plants and sessile invertebrates (personal observation). In the winter, waves act as agents of

disturbance with *Postelsia* as intermediaries since dislodged *Postelsia* often carry away with them the organisms they have overgrown. Organisms in the *Postelsia* understory are subject to extreme disturbances both in summer (if they are overgrown and smothered) and in winter (if they are only partially overgrown, but detached from the rock by a dislodged sea palm). Even in this highly disturbed environment, the understory community may still contain a relatively high diversity of turfy algae since *Postelsia* holdfasts seldom occupy all available space on the substratum (even at high densities, where canopy cover reaches 100%). In this algal community, grazing limpets (primarily *Lottia pelta* and *Lottia digitalis*) are the most abundant "predators". In California, *Lottia pelta* living within the *Postelsia* zone feed mainly on, and seem to prefer, *Postelsia* and microscopic diatoms which occur on *Postelsia* stipes in late summer (Craig, 1968).

Studies of marine, subtidal "kelp forests" have shown that kelps affect understory species through shading and overgrowth. These effects have been experimentally examined through kelp removals, thinning of kelp densities and manipulations of kelp canopies, (Dayton et al. 1984, Reed and Foster 1984, Santelices and Ojeda 1984, Kennelly 1987 a, b, c, 1989). Grazers (particularly sea urchins) have also been shown to influence subtidal algal assemblages (Lawrence 1975, Foreman 1977, Mann 1977, Vadas 1977, Duggins 1980, Schiel 1982, North 1983, Dayton 1985). Because of *Postelsia*'s unique "tree-like" morphology and its ability to form a dense canopy, the *Postelsia* zone is essentially an intertidal kelp forest. Like its larger and more frequently studied subtidal kelp relatives, *Postelsia* may also influence its understory algal community through shading and

overgrowth. While *Lottia pelta*, the most abundant limpet in *Postelsia* zones, is known to preferentially graze *Postelsia*, this limpet's direct and indirect effects on the community at large have not been studied. The *Postelsia* zone is therefore an ideal system in which to examine the relative importances of competition, disturbance, and grazing in structuring a community dominated seasonally by a large, canopy-forming plant.

In this study, I addressed the following questions:

1. How does *Postelsia* holdfast overgrowth affect algal species diversity and composition in the understory community?
2. What effects do seasonal disturbances (*Postelsia* holdfast overgrowth and dislodgement) have on species diversity and composition in the algal understory community?
3. What is the pattern of recovery in the community following removal of *Postelsia*?
4. What are the effects of shading by the *Postelsia* canopy on the understory algal community?
5. What are the effects of limpet grazing (predation) on the densities and sizes of the dominant space occupier?
6. How does limpet grazing affect species abundances and diversity in the algal understory community?

To examine the effects of shading and overgrowth by *Postelsia* and limpet grazing on the understory algal community, I conducted controlled and replicated experiments in which I: 1) completely removed *Postelsia* from experimental areas; 2) reduced *Postelsia* densities; 3) removed the *Postelsia* canopy and 4) removed limpet grazers.

METHODS

Study site

This study was conducted at the South Point of Depoe Bay (SPDB) (44°49' N, 124°04' W) on the central Oregon coast. This site is a rocky (basalt) headland fully exposed to oceanic waves (Fig. IV.1). All experimental plots were located on steeply sloping rock surfaces (40°-80°) in the middle of the *Postelsia* zone. *Postelsia* beds range from approximately 2.2-3.0 m above mean lower low water (MLLW) along a northwest-facing rock surface which is exposed to strong waves and surf. The low intertidal at this site is dominated by several species of coralline algae, *Plocamium cartilagineum, Constantinea simplex,* and the kelps *Laminaria setchellii* and *Lessoniopsis littoralis.* The low-middle zone at this site is dominated by the mussel *Mytilus californianus* and the barnacle *Pollicipes polymerus.* The upper-middle zone is dominated by the sea palm, *Postelsia palmaeformis* in the late spring, summer and early fall and by a variety of "turfy" red understory algae in winter which are present in the *Postelsia* understory throughout the year (Table IV.1). The most common understory species are *Odonthalia* sp. (see Table IV.1, note c), *Corallina vancouveriensis, Hymenena flabelligera,* and *Microcladia borealis.* Sessile and mobile invertebrates are patchily present and the most abundant grazers in this zone are the limpets *Lottia pelta* and *Lottia digitalis* (Table IV.2). Although mussels are occasionally present in the vertically sloping upper-middle zone, they are very scarce and never form beds. The high

intertidal is dominated by *Iridaea cornucopiae* and tufts of *Endocladia muricata*.

POSTELSIA MANIPULATION

Experimental design

To examine the effects of shading, competition for space in the understory, and disturbance, I initiated an experiment in April 1991 in the middle of the *Postelsia* zone along a steeply sloping rocky area at SPDB. Experimental units were 1 m x 1 m square plots marked with stainless steel screws at the corners. The experimental design was a randomized block with four replicates. The blocks were separate sea palm aggregations located along the rocky slope from north to south. Each block included four plots, each with one of the following randomly assigned treatments: 1) All *Postelsia* removed, 2) *Postelsia* density reduced to 50% of natural density (thinned), 3) *Postelsia* at natural density (unmanipulated control), and 4) *Postelsia* at natural density with blades removed. In the *Postelsia* removal treatment, I removed all *Postelsia* from each plot starting in winter and/or spring when plants first appeared, and I maintained this manipulation throughout the year. In the *Postelsia* density reduction treatment, I counted the total number of plants present in each of the treatment plots and randomly removed 50% of those individuals in spring of each year. In the blade removal treatment I cut the blades off all the plants in each of the plots. I began the blade trimmings in spring and repeated as necessary throughout the year. I maintained all the

manipulations and censused the plots monthly from April 1991 until December 1992 (21 months). Manipulations in this experiment were then discontinued, and monthly monitoring was continued for another 11 months, ending in November 1993.

Data collection and analysis

I sampled percent covers of all understory species in the sixteen plots once each month using a 0.25 m^2 quadrat with 64 uniformly spaced points. The innermost 0.25 m^2 of each 1 m^2 plot was sampled to avoid edge effects. Percent covers of *Postelsia* and of all understory species were measured in each plot. I calculated two measures of species diversity for the algal understory community. The Shannon-Wiener function (H') combines two measures of diversity -- richness and evenness;

$$H' = - \sum_{i=1}^{S} (p_i) (\ln p_i) \qquad (1)$$

where S=number of species and p_i=proportion of total sample belonging to the *i*th species. In this function, both a greater number of species (richness) and a more even distribution among species (equitability or evenness) increase species diversity. An alternative measure of diversity, Simpson's index (D) is based on the probability of picking two organisms at random that are different species;

$$D = 1 - \sum_{i=1}^{S} (p_i)^2 \qquad (2)$$

where S=number of species and p_i=proportion of individuals of species i in the community. Simpson's index gives relatively little weight to the rare species and more weight to the common species. I calculated understory algal species diversity in each plot for each monthly census using both methods.

Postelsia is an annual plant, resulting in a strong seasonal pattern in *Postelsia* density and understory percent cover. The system is essentially "re-set" each winter when a new generation of *Postelsia* grow up from the previous year's spores. Due to these strong temporal patterns in abundance of *Postelsia* and understory species, I calculated seasonal means by grouping monthly data: winter (January, February and March), spring (April, May and June), summer (July August and September) and fall, (October, November and December). Each seasonal mean was based on the average of the monthly means.

A two-trials repeated measures analysis of variance using year [first manipulation year (1991) and second manipulation year (1992)] and season (spring, summer, fall, winter) as trials factors was employed to analyze the most common understory percent cover data and species diversity indices from each of the treatments over time. Diversity and percent cover data from the recovery year (1993) were also analyzed using a repeated measures analysis of variance over three seasons (spring, summer and fall). All the percent cover data were arcsin-square root transformed and diversity data were log transformed to achieve approximate normality. All statistical analyses were done using SYSTAT (Wilkinson 1990).

GRAZER MANIPULATION

Experimental design

To examine the effect of limpet grazing on the *Postelsia*-dominated algal community, I began an experiment in the middle of the *Postelsia* zone along a steeply sloping rocky area at SPDB near the *Postelsia* manipulations. The experiment lasted 32 months, from April 1991 to November 1993. The experimental units were 70 cm x 70 cm square plots marked at the corners with stainless steel screws. I established eight plots to which I randomly assigned one of two treatments (+ limpets or - limpets). The - limpet plots were areas in which I removed all limpets. I removed both *Lottia digitalis* and *Lottia pelta*, though most of the limpets in each plot were *Lottia pelta*. In summer 1991, I scraped borders (8 cm wide) around all the plots. These were effective in slowing the traffic of limpets in and out of plots between each of the censuses. The four remaining plots + limpet plots were unmanipulated and were controls for the limpet removals.

Data collection

Several population and community attributes were quantified during monthly censuses of each plot. Densities of limpets greater than 0.5 cm (longest shell axis) were estimated prior to removing these individuals from the limpet removal plots. To measure the percent cover of all algal species present in the plots, I conducted monthly samples using the same

method described for the *Postelsia* manipulations. Densities of *Postelsia* and the percent covers of all understory species were measured in each plot. Lengths of *Postelsia* stipes from ten plants randomly selected from each plot in both treatments during the summers of 1992 and 1993 were also measured.

Data analysis

I calculated seasonal means based on the monthly percent cover, density and diversity data. I analyzed these data using a repeated measures analysis of variance to compare *Postelsia* densities, species diversities and understory percent covers in the two treatments (+ limpets and - limpets) over the three year (11 season) period. I visually examined residual and normal probability plots and arcsin-square root transformed the percent cover data, and log transformed the density data to achieve approximate normality. Multiple contrasts within the repeated measures analysis were employed to determine the seasons in which the means were significantly different.

Stipe length data from 1992 and 1993 were analyzed using a repeated measures analysis of variance comparing average stipe lengths of *Postelsia* in the two treatments over each of the months sampled in that year. The data were approximately normally distributed with equal variances (Bartlett's test) and did not require transformation. I measured the relationship between limpet and *Postelsia* density (both log transformed) using linear regression. All statistical analyses were done using SYSTAT (Wilkinson 1990).

RESULTS

POSTELSIA MANIPULATION

Effects of *Postelsia* density

As expected, the percent cover of *Postelsia* in the manipulation years was strongly affected by the density treatment, season and year (Fig. IV.2a, Table IV.3). Effects due to the density treatment varied depending on the season, since there were very few *Postelsia* in winter and high densities in summer. In the thinning manipulation, 50% of the *Postelsia* were removed in spring of 1991 and 1992. *Postelsia* percent cover reflects the amount of space occupied by holdfasts, and this is not necessarily strongly correlated with *Postelsia* density, since isolated plants can often have larger holdfast areas than aggregated plants (personal observation). Effects of thinning on *Postelsia* percent cover were significant in fall 1991 and spring 1992, and the effects of *Postelsia* removal were significant over the entire manipulation period (Fig. IV.2a, Table IV.3). In the recovery year, thinned plots had significantly higher *Postelsia* abundances than unmanipulated plots in spring 1993 and removal plots had the lowest *Postelsia* abundances. Effects of season and the previously applied density treatments were significant in the recovery period. Bare rock space varied seasonally and inversely with *Postelsia* abundance (Fig. IV.2b). Effects of *Postelsia* density on bare rock space varied depending on year and season during the manipulation period, and there was significant spatial variation due to blocks (Table IV.3). Abundance of bare rock was highest in all

treatments in fall and winter, and decreased over all years in the *Postelsia* removal treatment. Bare rock space was generally low in all treatments in the recovery period, and was lowest in the *Postelsia* removal treatment.

Odonthalia abundance varied both in space (blocks) and time (seasons) during the manipulation period (Table IV.3). The effects of *Postelsia* density on *Odonthalia* abundance varied over seasons and years. In all treatments, *Odonthalia* was least abundant in fall and winter, and increased in abundance in spring and summer (Fig. IV.2c). Medium density plots had the lowest abundances of *Odonthalia*. High density plots peaked in abundance of *Odonthalia* in spring/summer (at times when *Postelsia* abundance also peaked). *Odonthalia* abundance in *Postelsia* removal plots varied almost sinusoidally over the three years with peaks in summer, and troughs in winter. In the recovery year, *Odonthalia* abundance was highest in high density plots, and lowest in medium density plots.

The abundance of *Corallina* was strongly affected by *Postelsia* removal, and plots without *Postelsia* had the highest abundances of *Corallina* over the entire manipulation period (Fig. IV.2d). *Corallina* abundance was significantly higher in thinned plots than high density plots in summer and fall 1991. *Corallina* abundance varied significantly with density of *Postelsia*, season and with spatial blocks (Table IV.3). Variation in *Corallina* abundance with season depended on *Postelsia* density, block, and year. *Corallina* abundance in the recovery year was also significantly affected by *Postelsia* density and season, and remained highest in the *Postelsia* removal treatment.

Hymenena abundance was significantly affected by *Postelsia* density, and varied spatially (over blocks) (Table IV.3). Effects of *Postelsia* density on *Hymenena* abundance varied seasonally, and *Hymenena* was most abundant in high and medium *Postelsia* treatments in spring and summer (Fig. IV.2e). Abundance of *Hymenena* in *Postelsia* removal treatments was significantly lower than in high and medium density treatments in spring and summer of 1991 and 1992. Abundances of *Hymenena* were similar in all treatments in the recovery period, but *Hymenena* abundance was still significantly lowest in the *Postelsia* removal in fall 1993.

The pattern of *Microcladia* abundance was similar to that of *Corallina* with regards to the effects of *Postelsia* density. *Microcladia* was most abundant in *Postelsia* removal plots over the manipulation period (Fig. IV.2f). *Microcladia* abundance varied significantly with density of *Postelsia*, season and with spatial blocks (Table IV.3). Effects of *Postelsia* density on *Microcladia* abundance varied temporally over both seasons and years. *Microcladia* was significantly more abundant in medium than in high density plots only in summer of 1992. There were no significant effects of *Postelsia* density on *Microcladia* in the recovery year, and abundances of *Microcladia* reached similar levels in all treatments by summer 1993.

The Shannon-Wiener index of species diversity was significantly affected by *Postelsia* density, spatial variation (blocks), temporal variation (seasons) and interactive effects of density with season, season and year, year and block and the combined interactive effects of density, season and year (Table IV.3). Diversity was lowest overall in the high *Postelsia* density plots and diversity decreased in these plots in spring and summer of both

years (Fig. IV.2g). Both medium and low density plots had significantly higher diversity than high density plots in spring 1992. Diversity was highest in the thinned plots in winter of 1992. Diversity in the recovery year varied temporally with season and spatially with blocks. Both medium and low density plots had significantly higher diversity than high density plots in spring 1993. Simpson's diversity index was significantly affected both spatially (blocks) and temporally (seasons) (Table IV.3). Seasonal effects also varied depending on block, year and the interaction of year and *Postelsia* density. Diversity was generally lowest in the high *Postelsia* density plots and decreased in the spring/summer (Fig. IV.2h). Thinned plots had significantly higher diversity than high density plots in summer and fall 1991 and removal plots had higher diversities than high density plots in spring and summer 1991 and spring and fall 1992. Diversity in the recovery year varied seasonally. Both medium and low density plots had significantly higher diversity than high density plots in spring 1993.

In summary, reductions in *Posteslia* densities resulted in increased abundances of both *Corallina* and *Microcladia*, two fast-growing, turfy understory algal species. *Corallina* dominated primary space in the absence of *Postelsia*, and may inhibit recruitment of *Postelsia*. There was significant spatial variation among blocks in the abundances of most understory species. Areas with reduced *Postelsia* densities had higher species diversities of understory algae than unmanipulated natural areas.

Effects of *Postelsia* canopy (shading)

The abundance of *Postelsia* was negatively affected in the blade removal treatment (presumably since much of the photosynthetic area was removed from plants, growth was inhibited and mortality was increased). Abundance of *Postelsia* in the - blade plots during the manipulation period varied depending on the treatment, year, season and the interaction of all three factors (Table IV.4). - Blade plots had significantly lower densities of *Postelsia* than + blade plots in fall 1991 and spring 1992 (Fig. IV.3a). *Postelsia* abundances in the recovery period were similar in both treatments, but were significantly affected by season. As expected, bare rock space varied inversely with *Postelsia* percent cover. Abundance of bare rock was significantly affected by the blade removal treatment and varied temporally (over seasons) and spatially (over blocks) (Table IV.4). Abundance of bare rock space was highest in both treatments in fall/winter and was higher in the + blade than - blade treatment (Fig. IV.3b). Bare rock space was generally low in the recovery year in both treatments and was significantly affected by spatial variation (blocks) and spatial variation over seasons.

Abundance of *Odonthalia* was significantly affected by *Postelsia* canopy, seasonal variation, spatial variation (blocks), and the temporal variation over years and seasons (Table IV.4). *Odonthalia* was significantly more abundant in the absence of a *Postelsia* canopy in fall and winter 1991 and summer 1992 (Fig. IV.3c). Both + and - blade treatments had essentially similar abundances of *Odonthalia* in the recovery year, though

there was still significant temporal (over seasons) and spatial variation (over blocks).

Corallina abundance varied both spatially (over blocks), temporally (over years and seasons) and spatial variation was dependent on season (Table IV.4). *Corallina* peaked in fall/winter and gradually increased in abundance over the years (Fig. IV.3d). Abundance of *Corallina* was not significantly affected by blade removal, however *Corallina* abundance in - blade plots was generally higher than in + blade plots in summer, 1991 and 1992. Both + and - blade treatments had essentially similar abundances of *Corallina* in the recovery year, though there was still significant temporal (over seasons) and spatial variation (over blocks).

Hymenena abundance was significantly affected by *Postelsia* canopy and varied temporally (over years) and spatially (over blocks) (Table IV.4). Yearly variation in *Hymenena* was significantly affected by blocks, seasons and the interactive effects of seasons with *Postelsia* canopy, and seasons with blocks. *Hymenena* abundances in - blade plots were significantly lower than in + blade plots in spring 1991 and summer 1992, but were higher in fall 1991 (Fig. IV.3e). Abundances of *Hymenena* in the recovery year were significantly affected by *Postelsia* canopy and - blade plots had significantly lower abundances of *Hymenena* than + blade plots in summer 1993. There were also significant temporal (over seasons) and spatial variation (over blocks) in the recovery period.

Microcladia abundance was significantly affected by *Postelsia* canopy, and blade removal resulted in increased *Microcladia* abundance during the manipulation period (Table IV.4, Fig. IV.3f). *Microcladia* abundance was significantly affected by seasonal variation (season and season x year) and

variation in *Microcladia* abundance due to *Postelsia* canopy depended on both season and the interaction of season x year. *Microcladia* abundance in the recovery year did not differ between the blade manipulation treatments and did not vary temporally.

The patterns for both Shannon-Wiener and Simpson's diversity indices were essentially similar (Figs. IV.3g & IV.3h). Both diversity measures varied temporally (with season and year) and temporal variation depended on the presence or absence of *Postelsia* canopy (Table IV.4). Diversity was generally higher in the - blade treatment, and this difference was significant for both diversity indices in spring 1992. Diversity in the recovery year was also generally highest in the - blade treatment and was significantly higher in this treatment in spring 1993. Diversity in the recovery period was significantly affected by seasonal variation.

In summary, *Microcladia* significantly increased in abundance following removal of the *Postelsia* canopy and seems to be negatively affected by shade, but the presence of *Hymenena* is facilitated by shade. Removal of the *Postelsia* canopy also had a positive effect on the understory algal diversity.

GRAZER MANIPULATION

Effectiveness of limpet removal

As in virtually all such experiments, total limpet exclusion was not possible. However, limpet migration into these areas between monthly censuses was not excessive, and the limpet removal plots had significantly

fewer limpets over the course of the experiment than the control plots, with the exception of spring and summer 1991. (Fig. IV.4, Table IV.5).

Effects of grazers on *Postelsia*

Postelsia density was significantly higher in - limpet plots than in + limpet plots except in spring and fall 1991 (Fig. IV.5, Table IV.5). The number of *Postelsia* in each treatment also varied seasonally. Densities were highest in the late winter and early spring, when the sporophytes first appeared on the rock and were several mm to several cm large. There is high mortality of small plants in the spring as small *Postelsia* are overgrown by the holdfasts of other larger *Postelsia*. Sea palms which do not have a secure attachment to the rock (usually those growing on understory algae as small sporophytes) are ripped from the rock by wave action as they grow larger, since the forces due to drag imposed by the moving water increase with plant size and eventually become greater than the tenacity of the plant to the substrate. Thus there is considerable "self-thinning" in sea palm aggregations from winter to fall. Plots with many small *Postelsia* in winter have lower densities of larger plants in summer.

Effects of the limpet removal treatment varied temporally and depended strongly on season (significant limpet x season interactions) (Table IV.5). The univariate and multivariate results were generally consistent. Limpet and *Postelsia* densities were inversely correlated from the spring and summer of 1992 and 1993 (Fig. IV.6). Mean stipe length of *Postelsia* in - limpet plots was significantly greater than + limpet plot plants in the spring and summer months of 1993 and in July and

November of 1992 (Fig. IV.7, Table IV.5). These results suggest that limpet grazing had a strong effect on both abundance and size of the sea palm and that the strength of this effect was a direct function of limpet density.

Percent cover of *Postelsia* in - limpet plots was significantly higher than in+ limpet plots following the summer of the first manipulation year, with the exception of fall 1992 and winter 1993 when *Postelsia* were not very abundant in either treatment due to the annual die off of this plant (Fig. IV.8a, Table IV.6). Percent cover of *Postelsia* decreased in the + limpet plots from 1991 to 1993, probably the result of interannual variation in sea palm recruitment. As expected, changes in bare rock varied inversely with *Postelsia* abundance (Fig. IV.8b). - Limpet plots generally had lower percent covers of bare space in spring and summer following the initial manipulation (1991), though these effects were not statistically significant due to the large interplot variances (Table IV.6).

Effects of grazers on understory algal abundance and diversity

Abundance of understory algae varied strongly with season (Table IV.6). Abundance of *Odonthalia*, the most common understory alga changed seasonally and reached a peak in both treatments in late summer and early spring (Fig. IV.8c). Significant effects of limpets were not seen until summer of 1992 when - limpet plots had significantly lower percent covers of *Odonthalia* in summer and fall of 1992 and had significantly higher percent covers of *Odonthalia* in winter of 1993. *Corallina*, the second most abundant understory alga increased in both treatments over the course of the experiment, and - limpet plots had significantly lower

percent covers of *Corallina* than + limpet plots in fall, 1991 and in all seasons following the winter 1992 (Fig. IV.8d, Table IV.6). *Hymenena*, the third most abundant understory alga, did not fluctuate seasonally in abundance, and there were no significant differences between treatments in percent cover of this leafy, red alga (Fig. IV.8e, Table IV.6). *Microcladia*, present in low abundance, was less abundant in - limpet plots than in + limpet plots in spring, summer and fall 1992 and 1993 (Fig. IV.8f, Table IV.6). In summary, *Postelsia* increased in abundance while three understory species (*Odonthalia*, *Corallina* and *Microcladia*) decreased in the absence of limpets, suggesting that limpets have strong direct negative effects on *Postelsia* and positive indirect effects on *Odonthalia*, *Corallina* and *Microcladia*.

The two measures of understory algal species diversity, Shannon-Wiener and Simpson's, showed essentially similar patterns (Figs. IV.8g & IV.8h, Table IV.6). Both measures of diversity increased in the + limpet plots from 1991 to 1993. Interestingly, *Postelsia* percent covers also decreased in the + limpet plots from 1991 to 1993. Thus, the yearly variation in species diversity is strongly affected by yearly variation in *Postelsia* density. Diversity did not differ between limpet treatments in 1991, but - limpet plots had significantly lower diversity in both the spring and summer of 1992 and 1993 (i.e., at times when *Postelsia* also reach peak abundances). In summary, limpets maintain plant diversity at higher levels than is seen in their absence. This occurs despite the annual disappearance of the apparent dominant, *Postelsia*.

DISCUSSION

POSTELSIA MANIPULATIONS

As mentioned earlier, *Postelsia* may affect the algal understory through competition (for light and space) and disturbance. Competition for light is most intense in summer months when the *Postelsia* canopy intercepts most of the available light. *Postelsia* is an intense competitor for space in spring and summer and their holdfasts can overgrow low lying turfy species in the understory. Areas with high sea palm densities are also highly disturbed in fall and winter when storm waves dislodge *Postelsia* and the organisms that *Postelsia* had overgrown. In the absence of sea palms, the disturbance rate in the understory should be relatively low, since most of the species are low-lying turfy algae which are not often dislodged by wave action (Paine 1988). Competition for space should be reduced due to the removal of the dominant competitor and competition for light should be minimal with no canopy species. *Postelsia* manipulations were designed to examine the response of the understory community in the relative absence of competition (for light and space) and disturbance in the *Postelsia* removal treatment, the response of the community to intermediate levels of these factors in the reduced *Postelsia* density treatment, and the response of the community to changes in light levels in the blade removal treatment.

Effects of *Postelsia* on the understory algal community

Percent cover of *Postelsia* in *Postelsia* thinned plots was significantly lower than that in control plots only in the spring of 1992. Although the density of plants in this treatment was thinned by 50%, holdfasts of isolated plants may cover more space than aggregated plants, mentioned earlier (Paine 1979, Holbrook et al. 1991). So canopy area and holdfast percent cover were not equally affected, although the density of plants was reduced by 50%. There was significant spatial variation among blocks for many of the algal understory species, particularly *Odonthalia* and *Hymenena.* As mentioned earlier, the blocks were arranged from north to south, were all approximately west-facing and probably received equal amounts of sun exposure. The main difference between blocks was probably in the degree of wave exposure. The northern-most blocks were slightly more protected from direct wave breaking at low tide levels due to the shallow slope in the subtidal area below these blocks which caused incoming waves to break further offshore (personal observation). The subtidal rock slope below the southern-most blocks was steeper, and waves tended to break higher on the shore in this area. *Hymenena* tended to be more common in the southern blocks, while *Odonthalia* was generally more abundant in the northern blocks.

Abundances of most understory species were not significantly different between control and thinned plots. Complete removal of *Postelsia* led to a dramatic increase in the abundances of both *Corallina* and *Microcladia,* which both outcompeted *Hymenena. Corallina* is well adapted to rapidly colonize recently cleared areas, and Stewart (1989)

identifies several features that allow *Corallina* to quickly invade and spread into cleared areas: 1) reproductive cells are released for long periods of time, 2) lateral growth from basal crusts increases the surface initially occupied by single thalli, 3) growth of new erect axes from persistent crusts can regenerate damaged thalli, and 4) *Corallina* may disperse by spores or vegetative propagation. New erect thalli can grow from old crusts where these persist, and spores can also be involved in repopulation of a denuded area. *Corallina* is often the first macroscopic species to recruit into bare areas in the *Postelsia* zone and can persist for years if not disturbed (personal observation). *Microcladia* also quickly occupied the area vacated by *Postelsia* and, like *Corallina,* has the ability to grow quickly and rapidly colonize cleared areas.

Both Shannon-Wiener and Simpson's diversity indices were higher in thinned plots during most of the experiment (Figs. IV.2g & IV.2h). High understory diversity at medium *Postelsia* densities may reflect the response of the community to an intermediate level of disturbance (Connell 1978, Sousa 1979). At high *Postelsia* densities, understory species are overgrown and outcompeted in summer and are ripped from the rock in winter. At very low *Postelsia* densities, highly competitive understory species such as *Corallina* spread and outcompete poorly competitive understory species. In the absence of winter disturbance (*Postelsia* dislodgment) poorly competitive or rare understory species are not able to settle and grow. At intermediate *Postelsia* densities (and thus intermediate levels of disturbance) competitive understory species are not able to dominate and patches of bare space are available for poorly competitive or rare species to invade.

Effects of Shading on the understory algal community

In seaweed communities, the development of a dense canopy that impedes light penetration can have a profound effect on the overall composition of the community. In subtidal systems, the canopy may limit recruitment and growth of other algae, but may benefit shade-adapted species in the understory assemblage. The usual consequence of removal or deterioration of the canopy is a major shift in community structure as understory or poorly competitive potential canopy species increase in abundance while canopy dependent species decline (Dayton 1975, Foster 1975, Southward and Southward 1978, Pearse and Hines 1979, Ambrose and Nelson 1982, Moreno and Sutherland 1982, Dayton et al. 1984, Ojeda and Santelices 1984, Reed and Foster 1984, Santelices and Ojeda 1984, Hawkins and Harkin 1985, Johnson and Mann 1986, Kennelly 1987,1989). Changes in understory species abundances due to canopy removals are most often attributable to differential photosynthetic light tolerances of understory algae.

Sun flecks (transient bursts of light that reach the understory when sunlight penetrates gaps in the canopy) can form a large portion of the daily irradiance reaching understory species in both terrestrial forests and marine kelp forests (Chazdon 1988, Pearcy 1988). In *Macrocystis* kelp forests, these flecks of light are temporally associated with the dominant wave period, and certain understory species have been shown to efficiently utilize light flecks of this particular duration and period (Wing et al. 1993). In *Postelsia* beds, Holbrook et al. (1991) found that photosynthetically active

radiation rapidly attenuated with increasing distance below the top of the canopy. Light flecks created in the understory as the canopy plants were moved by waves did not make measurable contributions to the irradiance levels in the understory, thus most *Postelsia* understory species are probably adapted to low light levels in summer conditions.

Since *Postelsia* is an annual plant, the light regime in the understory changes drastically between seasons. In the winter, understory plants are exposed to direct, but low intensity sunlight. In spring and fall when *Postelsia* canopies are only partially developed, understory plants are exposed to patchy areas of light. In summer, when light intensities are greatest and also when the potential effects of desiccation are most serious, plants are completely shaded under the *Postelsia* canopy and are also most likely to be overgrown.

As a slight artifact of the manipulation, plots in which blades were removed generally had lower percent covers of *Postelsia* than control plots (Fig. IV.3a). This was most likely a direct effect of the blade removal, since plants with trimmed blades had little remaining photosynthetic area and therefore, much lower growth rates than control plants. Blade regrowth was surprisingly rapid and blades on many plants were able to regrow several centimeters in the month following the trimming.

Removal of the *Postelsia* canopy affected abundances of *Odonthalia* and *Microcladia*, which were generally more common in blade removal plots during the manipulation period. There were no differences between treatments in the abundances of these species during the recovery period, suggesting that both species were negatively affected by shading and that they are poorly competitive in the shady understory. Abundance of

Corallina was not significantly affected by shading, but *Corallina* in blade removal plots in summer was often white and apparently bleached by the sun. *Hymenena* is a thin-bladed, delicate red alga, which also bleached easily in the absence of shade. *Hymenena* was less abundant in blade removal plots (Fig. IV.3e) and may be considered an obligate understory species, as defined by Dayton (1975). These are species which grow below the canopy and decrease in abundance through desiccation, excessive light or wave action when the canopy is removed. Diversity of the algal understory was generally higher in the blade removal plots, suggesting that the shade of the *Postelsia* canopy has a negative influence on the diversity of the understory. Although some shade-adapted species, such as *Hymenena* were outcompeted in direct summer sunlight, removal of the canopy allowed other non-shade adapted species such as *Odonthalia* and *Microcladia* to increase in abundance and allowed other rarer, light-requiring understory species to settle in the *Postelsia* zone in the absence of shade.

Community Recovery

Recovery of this algal community from the persistent perturbations in 1991 and 1992 was investigated in 1993. 1993 was a poor year in general for sea palm recruitment, and + *Postelsia* plots in 1993 had lower percent covers of *Postelsia* than all other years (Fig. IV.2a). Thinned plots showed the most dramatic recovery of sea palms and had significantly higher percent covers of *Postelsia* than the + *Postelsia* plots. It is possible that sea palms in the thinned plots were more "robust" than their high density

counterparts and were able to invest more of their resources in spore production. Also, at high *Postelsia* densities and percent covers, much of the primary space is covered by *Postelsia* holdfasts in summer which may prevent sea palm spores from settling on the rock, resulting in only moderate recruitment in the following year. Areas with lower *Postelsia* densities and percent covers may have a greater amount of "free" or non-*Postelsia* occupied space on the substrate available for spore settlement and recruitment in the following year. Abundances of most understory species in the treatment plots approached levels similar to the + *Postelsia* plots (though abundance of *Odonthalia* remained significantly lower in thinned plots and abundance of *Corallina* in the - *Postelsia* plots remained above that of + *Postelsia* plots in 1993).

Postelsia cover remained low in - *Postelsia* plots in 1993 (Fig. IV.2a). There are two factors which may be important in limiting their recovery in this treatment. Firstly, since *Postelsia* were removed from a 1 m^2 area for two years, these plots were only seeded with spores from plants outside the plots. *Postelsia* appear to have a very limited spore dispersal, and concentrations of spores drop off sharply at distances greater than 1 m from the parent plant (Dayton 1973). The second factor limiting recovery of these areas is the lack of seasonal disturbance. Since *Postelsia* were absent from these plots for two years, *Corallina* and *Microcladia* increased in abundance, thereby reducing the available bare space (see Fig. IV.6c). *Postelsia* can recruit and grow on algal turf, but usually only to a small size if the holdfast is not able to make contact with the bare rock at any point (Paine 1988). The drag produced by a small *Postelsia* plant in flow can rapidly exceed the strength of the understory plant to which it is attached.

Plots covered with *Corallina* are especially difficult for *Postelsia* to colonize. The articulated joints of *Corallina* rupture easily when subjected to mechanical stress, and *Corallina* has the capacity to recover rapidly from breakage (Paine 1979). I predict that in several years *Postelsia* will successfully re-invade these plots. This process will be hastened if storms or other disturbances periodically expose bare rock, and if nearby *Postelsia* densities remain high enough to deluge the plots with spores each year.

Effects of limpets on *Postelsia*

As indicated by the increased density of *Postelsia* in - limpet plots, limpets had a large negative effect on *Postelsia* abundance. There were slight differences in the density and percent cover of *Postelsia* between - and + limpet plots in 1991, and these differences became much greater in 1992 and 1993. Limpets had their greatest effect on *Postelsia* density in winter, when *Postelsia* were in the gametophyte and small sporophyte stages (i.e., microscopic to several mm tall). Limpets can probably consume entire *Postelsia* plants at this stage, and may also affect young *Postelsia* sporophytes by "bulldozing" them from the rock as they forage (Dayton 1971). In plots where limpets were removed, many of the young *Postelsia* sporophytes survived and eventually reproduced, which resulted in very high densities of *Postelsia* in each plot. When limpets were initially removed in spring 1991, sporophyte *Postelsia* plants were already large enough to avoid being entirely consumed by limpets (i.e. several centimeters tall). Although limpets cannot consume entire, large sporophytic *Postelsia*, they may nevertheless have some negative effects on

large plants. Craig (1968) found that *Lottia pelta* collected from a *Postelsia* zone fed mainly on *Postelsia*, and on diatoms and other epiphytic microscopic algae growing on the *Postelsia*. In this study, limpets were observed grazing on the stipes of adult *Postelsia* in summer and fall, and limpet grazing marks were apparent on most *Postelsia* in fall. Since sharp-ended nicks may result in sudden mechanical failure when stipes are bent by waves (Denny et al. 1989, Holbrook et al. 1991) it seems likely that limpet grazing may sometimes lead to stipe breakage.

Limpet grazing also produced shorter sea palms, as indicated by longer mean stipe lengths of *Postelsia* in - limpet plots (Fig. IV.7). These differences may be due only indirectly to limpets, through their effects on *Postelsia* density. Holdfast areas per plant are lower for aggregations than for isolated plants (Paine 1979). Moreover, like trees, which tend to grow long and slender when in dense stands (Holbrook and Putz 1989), aggregated *Postelsia* are taller (greater stipe length) and have narrower crowns than isolated individuals (Holbrook et al. 1991). Both light intensity and mechanical perturbation can influence stem morphology in woody plants (Larson 1963, Wilson and Archer 1977, 1979, King 1981). Plants in dense aggregations may reach larger sizes due to mechanical support provided by neighbors, increased growth rates due to reduced desiccation and/or a competitive response for access to light (Holbrook et al. 1991). Holbrook et al. (1991) measured water flow forces and light penetration inside and outside dense *Postelsia* aggregations and found that water velocities were not reduced in the dense stands, but photon flux densities were significantly reduced. The suggestion is that light intensity is probably a more important factor influencing the morphology of densely

aggregated *Postelsia* than wave forces. Hence, the taller morphology of *Postelsia* in - limpet plots seems likely to be a plastic response of the plant to an increase in density.

Effects of limpets on *Postelsia* were also evident in the patterns of primary percent cover of *Postelsia* (i.e. the percent of total understory cover occupied by *Postelsia* holdfasts). In plots without limpets, *Postelsia* monopolized up to 60% of the rock space (Fig. IV.8a). Area covered by *Postelsia* holdfasts was inversely proportional to the area of bare rock, and large peaks in the percent cover of *Postelsia* preceded large peaks in percent covers of bare rock (Figs. IV. 8a & IV.8b). When *Postelsia* were ripped from the rock in winter, they often removed large patches of the understory that were overgrown by their holdfasts (Paine 1979, 1988). Often fragments of understory algae, or basal portions of plants were left behind after the *Postelsia* were dislodged, which may have been able to reproduce or spread and occupy some of the bare space before *Postelsia* regained dominance in the spring.

Effects of grazing the understory algal community

To fully assess the relative importances of predation (grazing), competition, and disturbance, it would have been ideal to have conducted all experimental manipulations (blade removals, *Postelsia* thinnings and removals) in all orthogonal combinations with and without limpets. Available space was limited at this site, however and I was unable to conduct all possible treatment combinations at one site. In the present experimental design, I cannot test for the indirect effects of limpets on

understory species (i.e., the indirect effects of limpets on understory species through increases in *Postelsia* densities as opposed to the direct effects of limpet grazing on understory species). However, I believe that limpets had strong indirect positive effects on understory algal abundances and diversity and perhaps weak or minor direct negative effects (via grazing) on the understory community. I believe this to be true for several reasons.

Firstly, most of the understory species in this zone are red algae which may be unpalatable to grazers due to high concentrations of bromophenolic compounds which are believed to function as deterrents to herbivory (Hay 1986, Carlson et al. 1989, Paul 1992). Secondly, there were no significant differences in the abundances of the common understory species or in species diversity in the first year of the experiment (1991) when *Postelsia* abundances were also relatively unaffected by limpet removal. Understory algal abundances and species diversity decreased in the - limpet plots in the second and third years of the experiment following increases in the percent cover *Postelsia*. Finally, I observed the holdfasts of *Postelsia* overgrowing many of these low lying turfy species in summer and noticed bare, holdfast-shaped areas in winter where large patches of algae were torn from the rock.

Limpets, however also have negative direct effects on understory species. As limpets forage, they tend to clear bare areas on the rock partially due to feeding, but also due mainly to their "bulldozing" effect as they move about on the surface and push away or dislodge whatever may lie in their path (Dayton 1971). These direct limpet effects are evident in the pattern of bare rock percent cover (Fig. IV.8b). - Limpet plots had higher percent covers of *Postelsia* in spring/summer, and so had lower

abundances of bare space in these seasons. One might expect these peaks in *Postelsia* abundances in - limpet plots to be followed by large peaks in bare rock space in fall/winter. However + limpet plots had nearly equally large peaks of bare rock space in fall/winter and also had relatively high amounts of bare rock space in spring/summer. These persistent areas of bare space were created by limpet movements and were useful in censusing limpets each month. since one limpet could usually be found near the edge of each bare patch.

In both treatments, *Corallina* cover gradually increased over the course of the experiment (Fig. IV.8d). This may reflect normal annual variation or unusually low natural densities of *Postelsia* in 1993. The presence of *Corallina* can be facilitated by grazing (Paine and Vadas 1969, Paine 1979) and in this experiment *Corallina* was significantly more abundant in plots with limpets. This difference may be indirectly due to the lack of the positive effects of grazing on *Corallina,* the effects of overgrowth due to greater densities of *Postelsia* in - limpet plots or a combination of both factors. The low abundance of *Microcladia* in limpet removal plots in the spring and summer is also probably due to effects of *Postelsia* overgrowth. It is clear that *Postelsia* is a competitively dominant alga in this area and can easily overgrow and outcompete low lying turfy algae in the absence of limpet grazing. *Postelsia* was the only species which increased in the absence of limpets and was most likely a major prey of limpets at SPDB.

The Shannon-Wiener index of species diversity incorporates both species richness and evenness, and so plots which had high percent covers of *Postelsia* in the spring and summer (and therefore lower percent covers

of most turfy understory species) may have had lower diversities than plots with the same number of species, but with more even distributions. Although Simpson's index of species diversity gives less weight to rare species and more weight to common species, patterns for the two indices of diversity were very similar. There were no differences in diversity between limpet treatments in 1991, however diversity was lower in - limpet plots than + limpet plots in both spring and summer 1992 and 1993 when *Postelsia* were abundant, presumably due to shifts in dominance as *Postelsia* overgrew many understory species during these months.

Herbivores have been shown to increase plant species diversity (Harper 1969, Paine and Vadas 1969), decrease plant species diversity (Harper 1969) or both (Vadas 1968, Harper 1969, Paine and Vadas 1969, Lubchenco 1978, Hixon and Brostoff 1983). Lubchenco (1978) suggests that the key to understanding the variable results of herbivores on plant species diversity lies in understanding consumer prey preferences and competitive interactions among the plants themselves. For example, if an herbivore feeds on a competitive dominant, then intermediate densities of herbivores may result in the highest plant species diversity. At low grazer densities, the competitively dominant plant can monopolize space, and at high herbivore densities all species of plants may be over-grazed (Connell 1978, Lubchenco 1978, Hixon and Brostoff 1983). The idea that a consumer that feeds on a competitively dominant prey can increase diversity has been suggested by several authors (Paine 1966, Harper 1969, Hall et al. 1970, Patrick 1970, Paine 1971, MacArthur 1972, VanValen 1974). In this system, *Postelsia* is an annual, "short-lived" species, but can outcompete all understory species when it is present due to its ability to swamp the habitat

with reproductive spores in the late summer and its ability to overgrow all low-lying, "turfy" algae in spring and summer. Limpets in this system may be considered keystone predators in the sense that they seem to preferentially consume and control the abundance of *Postelsia*, which is a competitive dominant in summer (Paine 1969, 1974, Menge et al. 1994). At low limpet densities, *Postelsia* increased in abundance and overgrew and outcompeted many understory species, thereby reducing their abundances which resulted in low species diversity. Natural densities of limpets at this site may reflect an intermediate level of herbivory and, therefore maintain relatively high species diversity. At high densities many molluscan grazers including limpets are known to be territorial and actively expel other herbivores from their feeding areas (Stimson 1970, 1973; Underwood 1979, Branch 1981). *L. pelta* and *digitalis* are known to return to a "home" area following a feeding foray (Craig 1968, Miller 1968) and may expend effort on aggressive behavioral interactions rather than feeding at very high densities, so it is unlikely that even high limpet densities could eliminate *Postelsia* from this system.

CONCLUSIONS

The understory algal community in the *Postelsia* zone on steeply sloping or vertical surfaces differs in many ways from the horizontal mussel-dominated communities described by Dayton (1973) and Paine (1979, 1988). *Postelsia* that grow on vertical surfaces exist among a mixed turf of low-lying red algae. *Postelsia* seems to thrive here by reproducing prolifically and growing rapidly. The haptera of *Postelsia* can grow out

over the algal turf as long as the holdfast is in contact with the bare rock at some point. *Postelsia* are ripped from the rock in winter, and bare rock space is renewed when the *Postelsia* holdfasts dislodge sections of overgrown turf.

Predation, competition and disturbance all play important roles in structuring this community. Grazing limpets play a major role in maintaining high levels of diversity in the algal understory community. Limpets indirectly contribute to the high species diversity in the understory by grazing *Postelsia,* thereby decreasing its abundance and competitive advantage over other understory species. Competition for space in the understory is very intense and bare rock space is quickly occupied. Disturbances which dislodge *Postelsia* and many overgrown understory species from the rock each winter play an important role in maintaining a high level of diversity in the algal understory and in providing a suitable "foothold" for *Postelsia* to spread from year to year. These annual disturbances prevent the monopolization of space by fast growing turfy species like *Corallina,* and may provide other less competitive, and perhaps relatively rare species a chance to settle and grow.

TABLES

Table IV.1.

Macrophytic algae present in the *Postelsia* understory at SPDB. D = dominant (usually occupies >10% mean cover), C = common (usually occupies 1 -10% cover), S = scarce.

Taxon	Relative Abundance
Chlorophyta	
Cladophora columbiana	C
Phaeophyta	
Postelsia palmaeformis	D
Alaria nana	S
Analipus japonicus	S
Rhodophyta	
Bossiella plumosa	C
Callithamnion pikeanum	S
Constantinea simplex	S
Corallina vancouveriensis	D
Dilsea californica[a]	C
Endocladia muricata	C
Halymenia schizymenioides[a]	C
Hymenena flabelligera[b]	C
Hymenena multiloba[b]	C
Iridaea heterocarpa	C
Iridaea splendens	C
Microcladia borealis	C
"*Odonthalia*" sp.[c]	D
Plocamium cartilagineum	S
Plocamium violaceum	C
Polysiphonia hendryii	C
Serraticardia macmillanii	C
Schizymenia pacifica[a]	C
Fleshy crusts	S
Coralline crusts	S

[a]These red bladed species often occur in multispecific patches and are often difficult to distinguish in the field.

[b]These lobe bladed red species are also often difficult to distinguish in the field.

[c]The generic and specific taxonomic status of this plant which is similar in form to both *Odonthalia* and *Neorhodomela* is currently not known (G. Hansen, personal communication)

Table IV.2.

Sessile and mobile invertebrates present in the *Postelsia* understory at SPDB. Barnacles were usually overgrown by algae. Mussels were patchily present only in some plots, and limpets were relatively abundant in most plots.

Taxon	Relative Abundance
Anthopleura sp.	scarce
Balanus glandula	overgrown by algae
Chthamalus dalli	overgrown by algae
Halichondria panicea	overgrown by algae
Katharina tunicata	scarce
Lottia digitalis	present
Lottia pelta	abundant
Mytilus californianus[a]	patchily present
Mytilus trossulus[a]	scarce
Pollicipes polymerus	patchily present

[a]These are difficult to distinguish when they are small.

Table IV.3. Two trials repeated measures analysis of variance on the effect of *Postelsia* density, year and season on percent covers of *Postelsia*, Bare Rock, *Odonthalia*, *Corallina*, *Hymenena* and *Microcladia* and Shannon-Wiener and Simpson's indices of species diversity during the manipulation (1991-1992) = M and recovery (1993) = R periods. Sums of squares are type III. In the multivariate test, WL = Wilks' Lambda. D = density (of *Postelsia*), S = season, Y= year (1991,1992) and E = error.

REPEATED MEASURES ANALYSIS OF VARIANCE

			UNIVARIATE TEST								MULTIVARIATE TEST				
			BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Postelsia	M	D	2	1.388	47.869	**<0.001**	Y	1	0.144	5.618	**0.030**	S	3,15	0.368	8.569	**0.001**
% cover		E	17	0.029			S	3	0.333	13.778	**<0.001**	S*D	6,30	0.367	3.249	**0.014**
							Y*D	2	0.001	0.050	0.952	Y*S	3,15	0.462	5.822	**0.008**
							S*D	6	0.087	3.583	**0.005**	Y*S*D	6,30	0.522	1.918	0.110
							Y*S	3	0.140	6.906	**0.001**					
							Y*S*D	6	0.040	1.980	0.086					
							E	51	0.020							
	R	D	2	0.227	7.003	**0.007**	S	2	0.285	60.491	**<0.001**	S	2,14	0.146	40.904	**<0.001**
		E	15	0.032			S*D	4	0.018	3.868	**0.012**	S*D	4,28	0.560	2.351	0.078
							E	30	0.005							
Bare Rock	M	D	2	0.004	0.215	0.808	Y	1	0.044	3.684	0.068	S	3,20	0.401	9.976	**<0.001**
% cover		B	3	0.124	6.880	**0.002**	S	3	0.137	6.124	**0.001**	S*D	6,40	0.463	3.134	**0.013**
		E	22	0.018			Y*D	2	0.230	19.205	**<0.001**	S*B	9,48	0.679	0.935	0.504
							Y*B	3	0.005	0.414	0.744	Y*S	3,20	0.747	2.260	0.113
							S*D	6	0.048	2.142	0.060	Y*S*D	6,40	0.562	2.229	0.060
							S*B	9	0.026	1.148	0.343	Y*S*B	9,48	0.655	1.032	0.429
							Y*S	3	0.049	3.138	0.031					
							Y*S*D	6	0.047	2.989	0.012					
							Y*S*B	9	0.010	0.625	0.772					
							E	66	0.016							
	R	D	2	0.045	3.175	0.066	S	2	0.014	1.594	0.217	S	2,17	0.843	1.579	0.235
		B	3	0.053	3.788	**0.029**	S*D	4	0.009	1.030	0.405	S*D	4,34	0.784	1.098	0.373
		E	8	0.014			S*B	6	0.007	0.810	0.569	S*B	6,34	0.807	0.639	0.698
							E	36	0.009							

Table IV.3 (Continued)

				UNIVARIATE TEST								MULTIVARIATE TEST				
				BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Odonthalia	M	D	2	0.263	1.262	0.313	Y	1	0.000	0.000	0.989	S	3,12	0.253	11.784	**0.001**
% cover		B	3	1.631	7.822	**0.003**	S	3	0.115	9.716	**<0.001**	S*D	6,24	0.377	2.510	**0.050**
		E	14	0.209			Y*D	2	0.004	0.226	0.801	S*B	9,29	0.358	1.714	0.130
							Y*B	3	0.006	0.337	0.799	Y*S	3,12	0.390	6.263	**0.008**
							S*D	6	0.038	3.238	**0.010**	Y*S*D	6,24	0.292	3.408	**0.014**
							S*B	9	0.014	1.179	0.333	Y*S*B	9,29	0.616	0.717	0.689
							Y*S	3	0.038	5.276	**0.004**					
							Y*S*D	6	0.022	3.027	**0.015**					
							Y*S*B	9	0.005	0.693	0.711					
							E	42	0.007							
	R	D	2	0.316	1.666	0.222	S	2	0.103	11.848	**<0.001**	S	2,14	0.293	16.867	**<0.001**
		E	15	0.190			S*D	4	0.004	0.503	0.734	S*D	4,28	0.848	0.600	0.665
							E	30	0.009							
Corallina	M	D	2	0.847	12.949	**0.001**	Y	1	0.024	4.574	0.051	S	3,12	0.078	47.356	**<0.001**
% cover		B	3	0.414	6.326	**0.006**	S	3	0.299	38.973	**<0.001**	S*D	6,24	0.351	2.752	**0.035**
		E	14	0.065			Y*D	2	0.012	2.314	0.135	S*B	9,29	0.204	3.000	**0.012**
							Y*B	3	0.001	0.179	0.909	Y*S	3,12	0.280	10.292	**0.001**
							S*D	6	0.027	3.532	**0.006**	Y*S*D	6,24	0.533	1.477	0.228
							S*B	9	0.023	3.002	**0.007**	Y*S*B	9,29	0.515	1.024	0.445
							Y*S	3	0.026	5.558	**0.003**					
							Y*S*D	6	0.009	2.001	0.087					
							Y*S*B	9	0.007	1.526	0.170					
							E	42	0.005							
	R	D	2	0.178	4.323	**0.033**	S	2	0.142	27.934	**<0.001**	S	2,14	0.170	34.207	**<0.001**
		E	15	0.041			S*D	4	0.011	2.259	0.086	S*D	4,28	0.577	2.215	0.093
							E	30	0.005							

Table IV.3 (continued)

			UNIVARIATE TEST								MULTIVARIATE TEST				
			BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Hymenena	M	D	2	0.231	4.455	**0.032**	Y	1	0.000	0.001	0.975	S	3,12	0.924	0.327	0.806
% cover		B	3	1.300	25.050	**0.000**	S	3	0.008	0.527	0.666	S*D	6,24	0.177	5.494	**0.001**
		E	14	0.052			Y*D	2	0.000	0.039	0.962	S*B	9,29	0.293	2.138	0.058
							Y*B	3	0.003	0.362	0.782	Y*S	3,12	0.938	0.263	0.850
							S*D	6	0.077	5.049	**0.001**	Y*S*D	6,24	0.897	0.224	0.965
							S*B	9	0.027	1.788	0.099	Y*S*B	9,29	0.219	2.824	**0.016**
							Y*S	3	0.001	0.138	0.937					
							Y*S*D	6	0.002	0.234	0.963					
							Y*S*B	9	0.014	2.064	0.055					
							E	42	0.007							
	R	D	2	0.017	1.533	0.255	S	2	0.050	5.019	**0.015**	S	2,11	0.650	2.956	0.094
		B	3	0.764	70.097	**0.000**	S*D	4	0.009	0.892	0.484	S*D	4,22	0.663	1.255	0.317
		E	12	0.011			S*B	6	0.003	0.255	0.952	S*B	6,22	0.798	0.437	0.846
							E	24	0.010							
Microcladia	M	D	2	0.416	12.908	**<0.001**	Y	1	0.028	3.887	0.061	S	3,20	0.339	12.977	**<0.001**
% cover		B	3	0.142	4.410	**0.014**	S	3	0.194	18.030	**<0.001**	S*D	6,40	0.582	2.070	0.079
		E	22	0.032			Y*D	2	0.026	3.603	**0.044**	S*B	9,48	0.517	1.687	0.118
							Y*B	3	0.017	2.372	0.098	Y*S	3,20	0.230	22.270	**<0.001**
							S*D	6	0.031	2.924	**0.014**	Y*S*D	6,40	0.549	2.331	**0.050**
							S*B	9	0.017	1.564	0.145	Y*S*B	9,48	0.901	0.237	0.987
							Y*S	3	0.318	34.028	**<0.001**					
							Y*S*D	6	0.031	3.269	**0.007**					
							Y*S*B	9	0.002	0.251	0.985					
							E	66	0.009							
	R	D	2	0.039	2.894	0.078	S	2	0.062	7.251	**0.002**	S	2,20	0.607	6.473	**0.007**
		E	21	0.014			S*D	4	0.003	0.328	0.857	S*D	4,40	0.950	0.262	0.901
							E	42	0.008							

Table IV.3 (Continued)

			UNIVARIATE TEST								MULTIVARIATE TEST				
			BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Shannon	M	D	2	0.174	8.354	**0.005**	Y	1	0.017	2.867	0.114	S	3,11	0.230	12.256	**0.001**
Diversity		B	3	0.106	5.072	**0.015**	S	3	0.060	12.689	**<0.001**	S*D	6,22	0.238	3.850	**0.009**
		E	13	0.021			Y*D	2	0.001	0.118	0.890	S*B	9,26	0.416	1.298	0.283
							Y*B	3	0.029	4.795	**0.018**	Y*S	3,11	0.468	4.172	**0.034**
							S*D	6	0.024	5.052	**0.001**	Y*S*D	6,22	0.218	4.178	**0.006**
							S*B	9	0.008	1.717	0.118	Y*S*B	9,26	0.283	2.034	0.075
							Y*S	3	0.020	6.005	**0.002**					
							Y*S*D	6	0.016	4.763	**0.001**					
							Y*S*B	9	0.010	2.848	**0.011**					
							E	39	0.003							
	R	D	2	0.054	3.288	0.073	S	2	0.602	78.919	**<0.001**	S	2,11	0.082	61.604	**<0.001**
		B	3	0.106	6.516	**0.007**	S*D	4	0.001	1.445	0.250	S*D	4,22	0.644	1.354	0.282
		E	12	0.016			S*B	6	0.089	11.713	**<0.001**	S*B	6,22	0.159	5.517	**0.001**
							E	24	0.008							
Simpson's	M	D	2	0.044	3.669	0.052	Y	1	0.002	1.827	0.198	S	3,12	0.287	9.956	**0.001**
Diversity		B	3	0.065	5.483	**0.011**	S	3	0.020	15.012	**<0.001**	S*D	6,24	0.530	1.493	0.223
		E	14	0.012			Y*D	2	0.002	1.676	0.223	S*B	9,29	0.291	2.158	0.056
							Y*B	3	0.004	3.158	0.058	Y*S	3,12	0.283	10.113	**0.001**
							S*D	6	0.002	1.457	0.216	Y*S*D	6,24	0.216	4.609	**0.003**
							S*B	9	0.004	2.993	**0.008**	Y*S*B	9,29	0.387	1.556	0.175
							Y*S	3	0.018	10.463	**<0.001**					
							Y*S*D	6	0.010	6.201	**<0.001**					
							Y*S*B	9	0.003	1.909	0.077					
							E	42	0.002							
	R	D	2	0.028	2.653	0.103	S	2	0.014	7.604	**0.002**	S	2,14	0.405	10.290	**0.002**
		E	15	0.011			S*D	4	0.003	1.463	0.238	S*D	4,28	0.704	1.345	0.278
							E	30	0.002							

Table IV.4. Two trials repeated measures analysis of variance on the effect of *Postelsia* canopy, year and season on percent covers of *Postelsia*, Bare Rock, *Odonthalia*, *Corallina*, *Hymenena* and *Microcladia* and Shannon-Wiener and Simpson's indices of species diversity during the manipulation (1991-1992) = M and recovery (1993) = R periods. Sums of squares are type III. In the multivariate test, WL = Wilks' Lambda. C = canopy (+/- blades), S = season, Y= year (1991,1992) and E = error.

REPEATED MEASURES ANALYSIS OF VARIANCE

			UNIVARIATE TEST								MULTIVARIATE TEST				
			BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Postelsia	M	C	1	0.633	43.524	<0.001	Y	1	0.156	4.859	0.046	S	3,11	0.302	8.486	0.003
% cover		E	13	0.015			S	3	0.420	18.070	<0.001	S*C	3,11	0.535	3.188	0.067
							Y*C	1	0.002	0.055	0.819	Y*S	3,11	0.549	3.013	0.076
							S*C	3	0.033	1.436	0.247	Y*S*C	3,11	0.335	7.272	0.006
							Y*S	3	0.091	3.943	0.015					
							Y*S*C	3	0.087	3.767	0.018					
							E	39	0.023							
	R	C	1	0.034	2.005	0.187	S	2	0.151	33.521	<0.001	S	2,9	0.147	26.136	<0.001
		E	10	0.017			S*C	2	0.005	1.158	0.334	S*C	2,9	0.814	1.025	0.397
							E	20	0.005							
Bare Rock	M	C	1	0.108	5.750	0.031	Y	1	0.000	0.019	0.893	S	3,12	0.220	14.161	<0.001
% cover		B	3	0.086	4.614	0.019	S	3	0.157	5.143	0.004	S*C	3,12	0.771	1.186	0.356
		E	14	0.019			Y*C	1	0.024	1.933	0.186	S*B	9,29	0.566	0.861	0.569
							Y*B	3	0.018	1.500	0.258	Y*S	3,12	0.786	1.088	0.391
							S*C	3	0.026	0.851	0.474	Y*S*C	3,12	0.778	1.139	0.373
							S*B	9	0.026	0.865	0.563	Y*S*B	9,29	0.530	0.973	0.482
							Y*S	3	0.033	2.028	0.125					
							Y*S*C	3	0.029	1.809	0.160					
							Y*S*B	9	0.011	0.653	0.746					
							E	42	0.016							
	R	C	1	0.030	5.251	0.043	S	2	0.010	1.529	0.239	S	2,10	0.603	3.291	0.080
		B	3	0.108	19.148	<0.001	S*C	2	0.001	0.176	0.840	S*C	2,10	0.913	0.479	0.633
		E	11	0.006			S*B	6	0.009	1.479	0.231	S*B	6,20	0.283	2.930	0.032
							E	22	0.006							

Table IV.4 (Continued)

			UNIVARIATE TEST								MULTIVARIATE TEST			
			BETWEEN SUBJECTS				WITHIN SUBJECTS							
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Odonthalia	M	C	1	0.365	5.502	**0.041**	Y	1	0.007	0.312	0.589	S	3,8	0.233	8.789	**0.007**
% cover		B	3	2.155	32.534	**<0.001**	S	3	0.181	10.495	**<0.001**	S*C	3,8	0.613	1.683	0.247
		E	10	0.066			Y*C	1	0.046	2.044	0.183	S*B	9,19	0.436	0.886	0.554
							Y*B	3	0.006	0.284	0.836	Y*S	3,8	0.234	8.732	**0.007**
							S*C	3	0.034	1.978	0.138	Y*S*C	3,8	0.438	3.423	0.073
							S*B	9	0.016	0.950	0.499	Y*S*B	9,19	0.318	1.310	0.293
							Y*S	3	0.067	6.497	**0.002**					
							Y*S*C	3	0.017	1.700	0.188					
							Y*S*B	9	0.010	1.017	0.449					
							E	30	0.010							
	R	C	1	0.016	0.240	0.639	S	2	0.072	19.378	**<0.001**	S	2,6	0.105	25.577	**0.001**
		B	3	0.482	7.016	**0.016**	S*C	2	0.006	1.562	0.244	S*C	2,6	0.683	1.390	0.319
		E	7	0.069			S*B	6	0.010	2.708	0.058	S*B	6,12	0.278	1.792	0.184
							E	14	0.004							
Corallina	M	C	1	0.006	0.099	0.760	Y	1	0.099	13.305	**0.004**	S	3,8	0.052	48.270	**<0.001**
% cover		B	3	0.425	6.721	**0.009**	S	3	0.177	20.517	**<0.001**	S*C	3,8	0.415	3.757	0.060
		E	10	0.063			Y*C	1	0.000	0.026	0.876	S*B	9,19	0.066	4.480	**0.003**
							Y*B	3	0.014	1.877	0.197	Y*S	3,8	0.433	3.498	0.070
							S*C	3	0.031	3.579	**0.025**	Y*S*C	3,8	0.804	0.649	0.605
							S*B	9	0.030	3.444	**0.005**	Y*S*B	9,19	0.449	0.851	0.581
							Y*S	3	0.015	1.346	0.278					
							Y*S*C	3	0.008	0.677	0.573					
							Y*S*B	9	0.012	1.046	0.428					
							E	30	0.011							
	R	C	1	0.029	1.571	0.250	S	2	0.042	12.852	**0.001**	S	2,6	0.133	19.540	**0.002**
		B	3	0.118	6.410	**0.020**	S*C	2	0.000	0.101	0.905	S*C	2,6	0.968	0.100	0.907
		E	7	0.018			S*B	6	0.006	1.796	0.172	S*B	6,12	0.261	1.913	0.160
							E	14	0.003							

Table IV.4 (Continued)

				UNIVARIATE TEST								MULTIVARIATE TEST			
				BETWEEN SUBJECTS				WITHIN SUBJECTS							
Category	Period		df	MS	F	p		df	MS	F	p	df	WL	F	p
Hymenena	M	C	1	0.090	5.382	**0.043**	Y	1	0.009	5.368	**0.043**	S 3,8	0.558	2.116	0.176
% cover		B	3	1.343	80.616	**<0.001**	S	3	0.023	2.473	0.081	S*C 3,8	0.468	3.028	0.093
		E	10	0.017			Y*C	1	0.005	3.130	0.107	S*B 9,19	0.260	1.610	0.181
							Y*B	3	0.008	4.892	**0.024**	Y*S 3,8	0.239	8.508	**0.007**
							S*C	3	0.028	3.035	**0.044**	Y*S*C 3,8	0.272	7.132	**0.012**
							S*B	9	0.018	1.912	0.089	Y*S*B 9,19	0.133	2.810	**0.027**
							Y*S	3	0.031	5.827	**0.003**				
							Y*S*C	3	0.012	2.292	0.098				
							Y*S*B	9	0.016	3.021	**0.011**				
							E	30	0.005						
	R	C	1	0.053	14.536	**0.007**	S	2	0.042	7.816	**0.005**	S 2,6	0.255	8.770	**0.017**
		B	3	0.643	176.627	**<0.001**	S*C	2	0.007	1.339	0.294	S*C 2,6	0.452	3.632	0.093
		E	7	0.004			S*B	6	0.006	1.211	0.357	S*B 6,12	0.258	1.937	0.155
							E	14	0.005						
Microcladia	M	C	1	0.227	13.884	**0.002**	Y	1	0.001	0.165	0.690	S 3,15	0.199	20.134	**<0.001**
% cover		E	17	0.016			S	3	0.174	28.627	**<0.001**	S*C 3,15	0.580	3.616	**0.038**
							Y*C	1	0.051	6.980	**0.017**	Y*S 3,15	0.218	17.953	**<0.001**
							S*C	3	0.019	3.058	**0.036**	Y*S*C 3,15	0.490	5.195	**0.012**
							Y*S	3	0.306	36.557	**<0.001**				
							Y*S*C	3	0.035	4.191	**0.010**				
							E	51	0.008						
	R	C	1	0.010	0.810	0.383	S	2	0.021	3.810	**0.034**	S 2,13	0.647	3.544	0.059
		E	14	0.012			S*C	2	0.001	0.226	0.799	S*C 2,13	0.969	0.211	0.813
							E	28	0.006						

Table IV.4 (Continued)

				UNIVARIATE TEST								MULTIVARIATE TEST				
				BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	WL	F	p
Shannon	M	C	1	0.093	2.242	0.160	Y	1	0.077	6.172	**0.029**	S	3,10	0.109	27.370	**<0.001**
diversity		E	12	0.041			S	3	0.133	30.186	**<0.001**	S*C	3,10	0.825	0.707	0.569
							Y*C	1	0.022	1.730	0.213	Y*S	3,10	0.590	2.316	0.138
							S*C	3	0.003	0.598	0.620	Y*S*C	3,10	0.362	5.867	**0.014**
							Y*S	3	0.008	1.282	0.295					
							Y*S*C	3	0.021	3.359	**0.029**					
							E	36	0.006							
	R	C	1	0.102	3.071	0.110	S	2	0.021	7.507	**0.004**	S	2,9	0.461	5.263	**0.031**
		E	10	0.033			S*C	2	0.006	2.019	0.159	S*C	2,9	0.752	1.484	0.277
							E	20	0.003							
Simpson's	M	C	1	0.034	1.764	0.209	Y	1	0.022	5.442	**0.038**	S	3,10	0.126	23.064	**<0.001**
diversity		E	12	0.020			S	3	0.049	30.387	**<0.001**	S*C	3,10	0.662	1.703	0.229
							Y*C	1	0.006	1.452	0.251	Y*S	3,10	0.518	3.103	0.076
							S*C	3	0.003	2.090	0.119	Y*S*C	3,10	0.382	5.400	**0.018**
							Y*S	3	0.003	1.467	0.240					
							Y*S*C	3	0.006	2.871	**0.050**					
							E	36	0.002							
	R	C	1	0.054	4.088	0.071	S	2	0.010	15.712	**<0.001**	S	2,9	0.244	13.912	**0.002**
		E	10	0.013			S*C	2	0.001	2.367	0.120	S*C	2,9	0.687	2.051	0.185
							E	20	0.001							

Table IV.5. Repeated measures analysis of variance on the effect of limpet removal and season on limpet density and *Postelsia* density and the effect of limpet removal and month on *Postelsia* stipe lengths. Sums of squares are type III. In the multivariate test, WL = Wilks' Lambda. L = limpet treatment (+/- limpets), S = season, M = month, and E = error.

REPEATED MEASURES ANALYSIS OF VARIANCE

			UNIVARIATE TEST									MULTIVARIATE TEST			
			BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category	Period		df	MS	F	p		df	MS	F	p		df	MS	F	p
Limpet	91-93	L	1	63.575	94.866	<0.001	S	10	4.057	14.432	<0.001	S	10,5	0.004	115.923	<0.001
density		E	14	0.670			LxS	10	1.285	4.572	<0.001	LxS	10,5	0.050	9.448	0.011
							E	140	0.281							
Postelsia	91-93	L	1	72.475	96.582	<0.001	S	10	15.469	35.390	<0.001	S	10,5	0.017	28.670	0.001
density		E	14	0.750			LxS	10	2.620	5.995	<0.001	LxS	10,5	0.087	5.257	0.040
								E	140	0.437						
Stipe	1992	L	1	757.480	18.258	<0.001	M	2	412.182	10.743	<0.001	M	2,42	0.557	16.726	<0.001
Lengths		E	43	41.487			LxM	2	145.307	3.787	0.027	LxM	2,42	0.734	7.595	0.002
							E	86	38.368							
	1993	L	1	2100.787	125.832	<0.001	M	4	1004.507	73.057	<0.001	M	4,50	0.216	45.313	<0.001
		E	53	16.695			LxM	4	27.090	1.970	0.100	LxM	4,50	0.873	1.818	0.140
							E	212	13.750							

Table IV.6. Repeated measures analysis of variance on the effect of limpet removal and season on percent covers of *Postelsia*, Bare Rock, *Odonthalia*, *Corallina*, *Hymenena* and *Microcladia* and Shannon-Wiener and Simpson's indices of species diversity. Sums of squares are type III. In the multivariate test, WL = Wilks' Lambda. L = limpet treatment (+/- limpets), S = season, and E = error.

REPEATED MEASURES ANALYSIS OF VARIANCE

		UNIVARIATE TEST								MULTIVARIATE TEST				
		BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category		df	MS	F	p		df	MS	F	p		df	MS	F	p
Postelsia	L	1	2.079	58.592	**<0.001**	S	10	0.632	31.593	**<0.001**	S	10,5	0.022	22.487	0.002
% cover	E	14	0.035			LxS	10	0.085	4.272	**<0.001**	LxS	10,5	0.042	11.300	0.008
						E	140	0.020							
Bare Rock	L	1	0.003	0.251	0.624	S	10	0.345	38.266	**<0.001**	S	10,5	0.014	34.534	0.001
% cover	E	14	0.010			LxS	10	0.002	0.252	0.990	LxS	10,5	0.665	0.252	0.970
						E	140	0.009							
Odonthalia	L	1	0.011	0.386	0.545	S	10	0.111	11.774	**<0.001**	S	10,5	0.043	11.174	<0.001
% cover	E	14	0.029			LxS	10	0.035	3.749	**<0.001**	LxS	10,5	0.106	4.203	0.063
						E	140	0.009							
Corallina	L	1	0.563	20.450	**<0.001**	S	10	0.133	22.757	**<0.001**	S	10,5	0.016	30.897	0.001
% cover	E	14	0.028			LxS	10	0.015	2.485	**0.009**	LxS	10,5	0.297	1.183	0.452
						E	140	0.006							
Hymenena	L	1	0.022	0.610	0.448	S	10	0.032	4.912	**<0.001**	S	10,5	0.158	2.664	0.146
% cover	E	14	0.037			LxS	10	0.003	0.482	0.900	LxS	10,5	0.565	0.385	0.907
						E	140	0.006							
Microcladia	L	1	0.222	18.012	**0.001**	S	10	0.019	2.830	**0.003**	S	10,5	0.099	4.531	0.055
% cover	E	14	0.012			LxS	10	0.012	1.766	0.072	LxS	10,5	0.212	1.858	0.256
						E	140	0.007							

Table IV.6 (Continued)

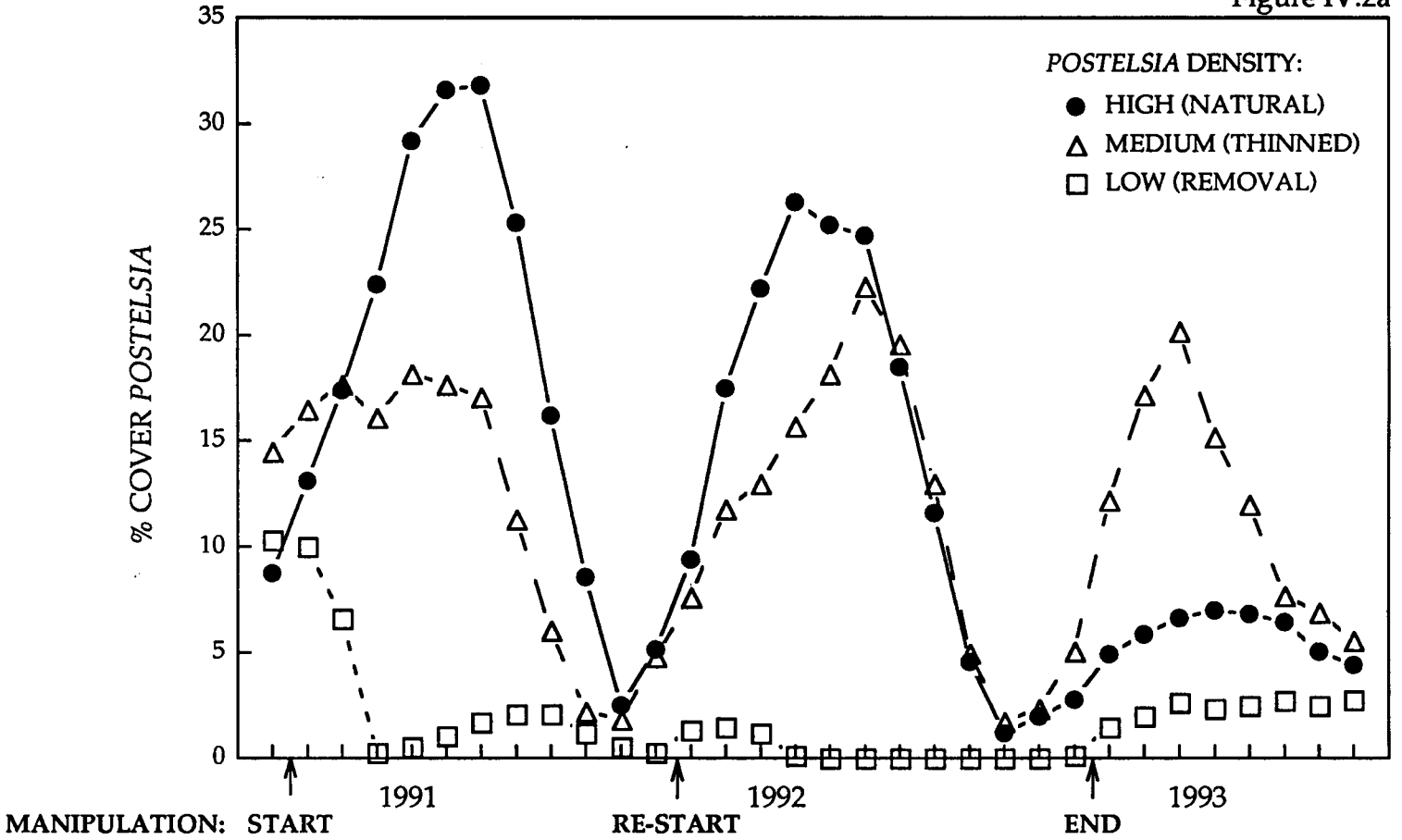
		UNIVARIATE TEST								MULTIVARIATE TEST				
		BETWEEN SUBJECTS				WITHIN SUBJECTS								
Category		df	MS	F	p		df	MS	F	p		df	MS	F	p
Shannon (H')	L	1	0.270	6.131	**0.027**	S	10	0.121	9.700	**<0.001**	S	10,5	0.047	10.052	**0.010**
diversity	E	14	0.044			LxS	10	0.013	1.055	0.401	LxS	10,5	0.161	2.608	0.151
						E	140	0.012							
Simpson's (D)	L	1	0.150	6.239	**0.026**	S	10	0.065	12.432	**<0.001**	S	3,20	0.013	39.369	**<0.001**
diversity	E	14	0.024			LxS	10	0.006	1.064	0.394	LxS	3,20	0.104	4.295	0.061
						E	140	0.005							

FIGURES

Figure IV.1. The experimental site at SPDB in spring, showing a dense cover of *Postelsia* in the middle zone.

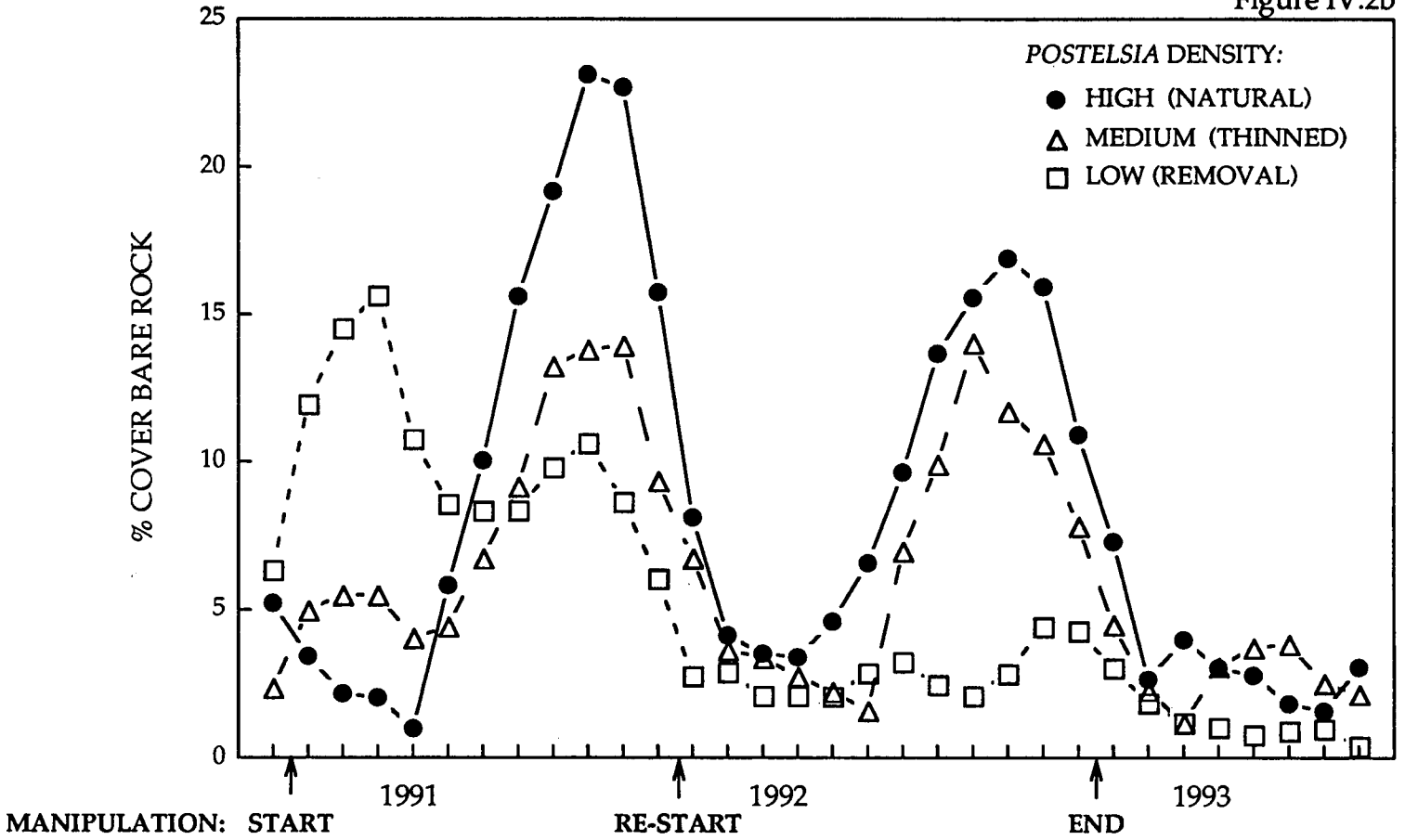
Figure IV.2. Mean primary percent cover of: (a) *Postelsia*, (b) Bare rock, (c) *Odonthalia*, (d) *Corallina*, (e) *Hymenena*, and (f) *Microcladia* and (g) mean Shannon-Wiener species diversity and (h) Simpson's species diversity in unmanipulated, natural *Postelsia* density plots (solid circles), thinned *Postelsia* density plots (open triangles), and *Postelsia* removal plots (open squares). Graphs are moving averages (over three consecutive dates) of monthly census data. The first treatment point represents a pre-treatment date. Error bars are not shown for monthly averages, however significance levels based on multiple comparisons between treatments in a repeated measures ANOVA are shown below each graph. Thinning effects are differences between the high and medium density treatments, and removal effects are differences between the high and low density treatments. Multiple comparisons were done within seasons, where WI = winter (January, February and March), SP = spring (April, May and June), SU = summer (July, August and September) and FA = fall (October, November and December). *=$p<0.05$, **=$p<0.01$.

Figure IV.2a



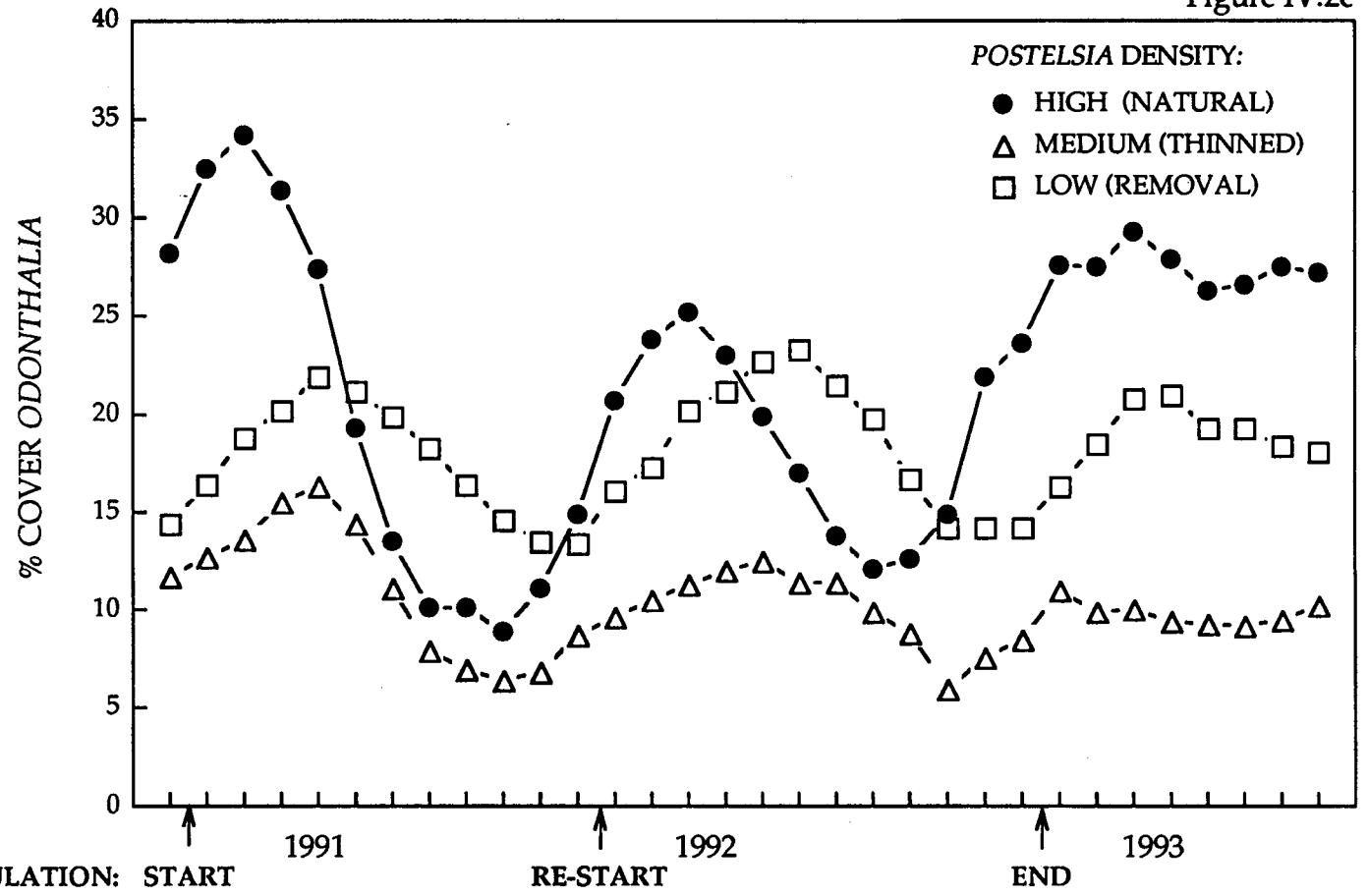
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	NS	*	NS	*	NS	NS	NS	*	NS	NS
REMOVAL	*	**	**	*	**	**	**	NS	NS	NS	*

Figure IV.2b



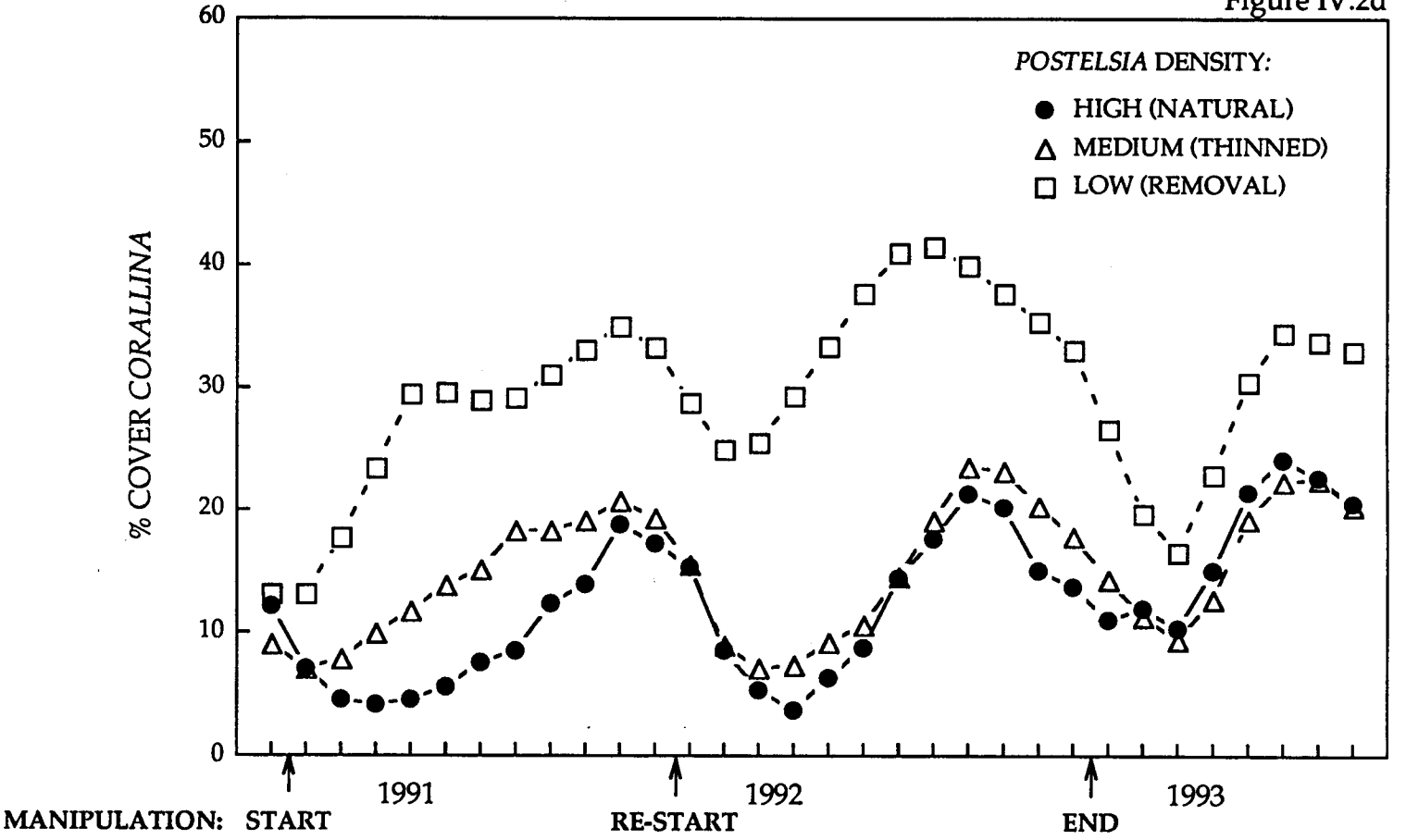
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
REMOVAL	**	*	NS	NS	NS	NS	**	NS	NS	*	NS

Figure IV.2c



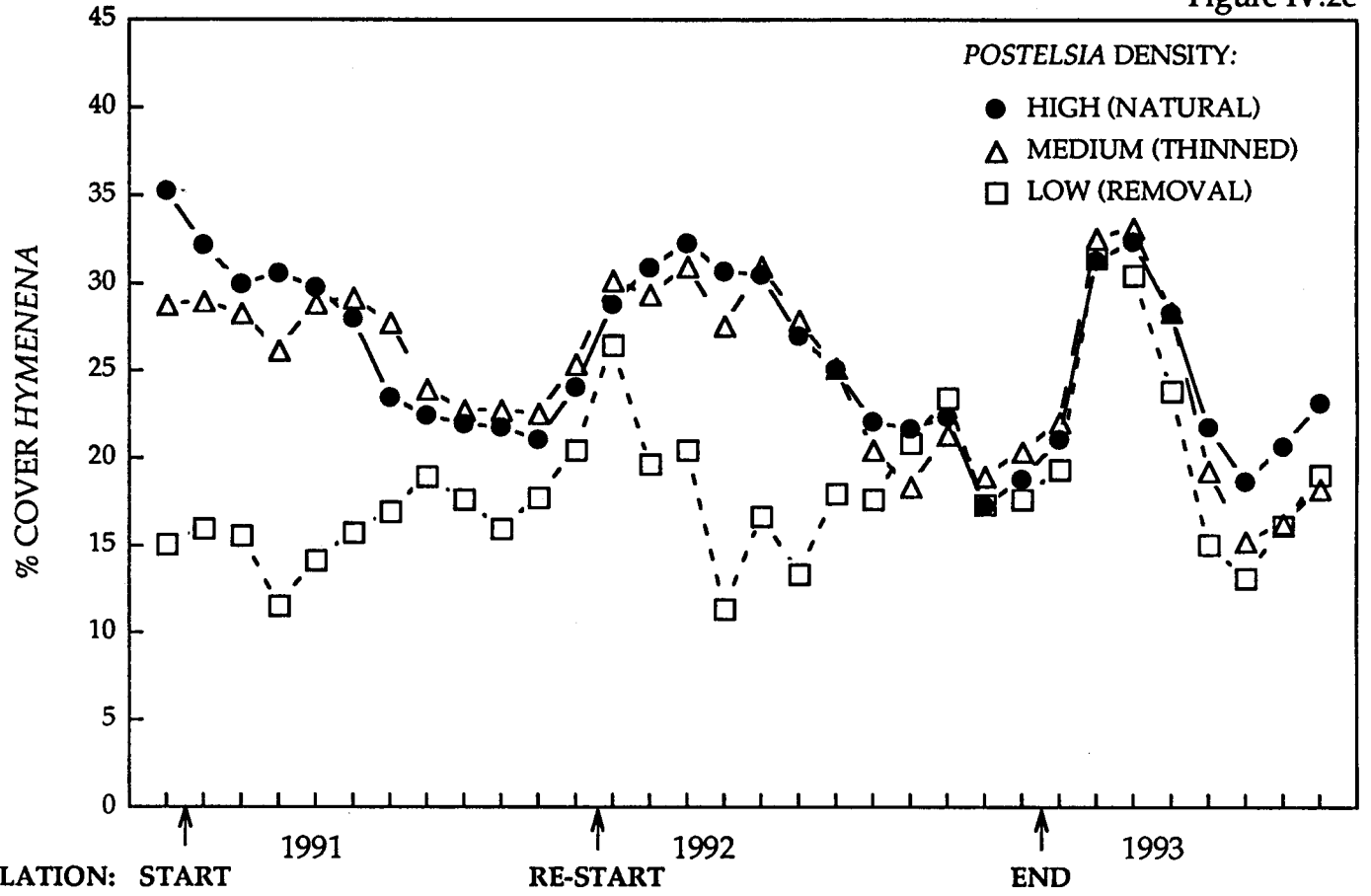
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	*	NS	NS	NS	NS	NS	NS	NS	*	NS	NS
REMOVAL	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Figure IV.2d



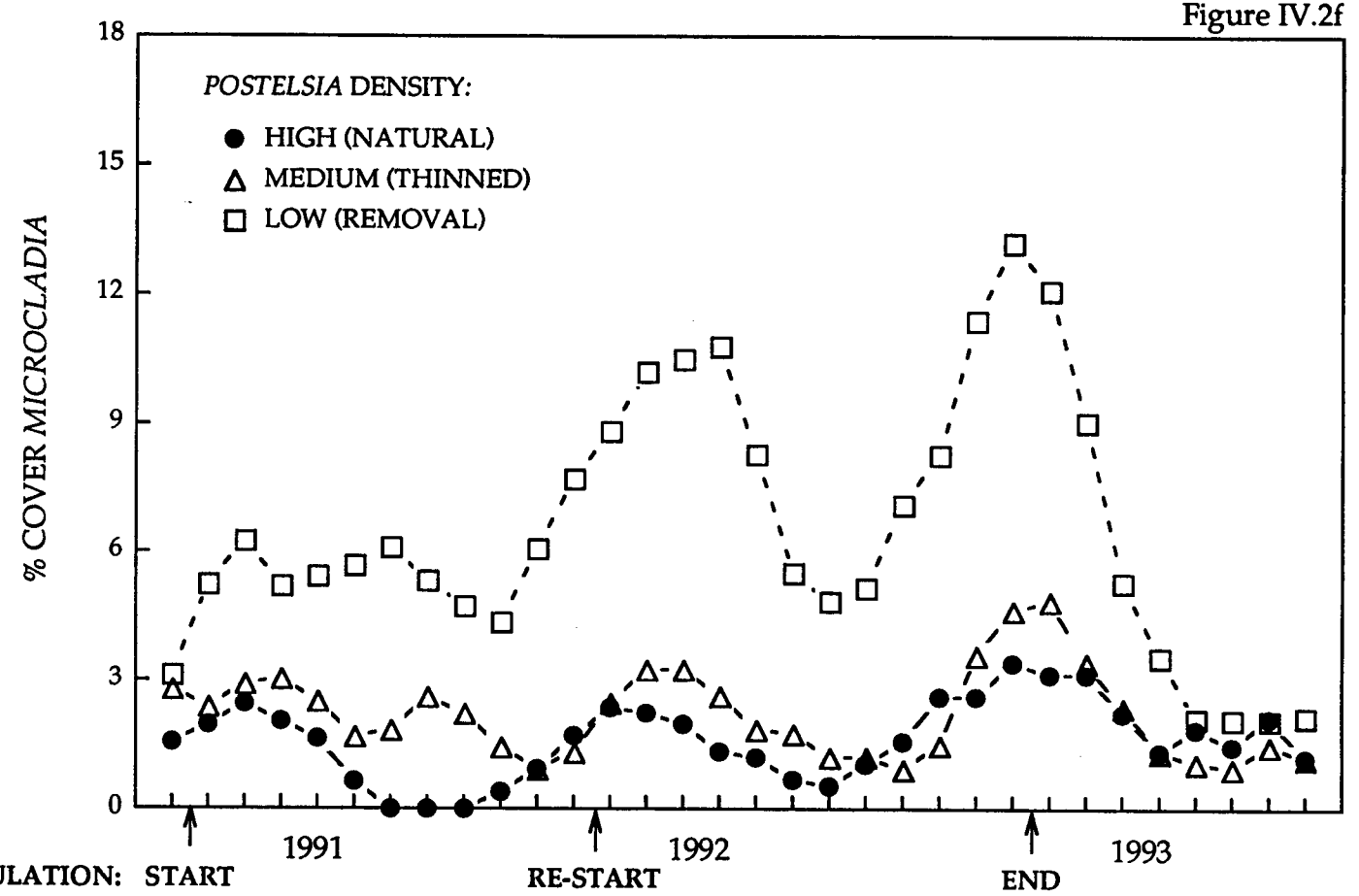
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	**	**	NS	NS	NS	NS	NS	NS	NS	NS
REMOVAL	**	**	**	**	**	**	**	*	NS	NS	**

Figure IV.2e



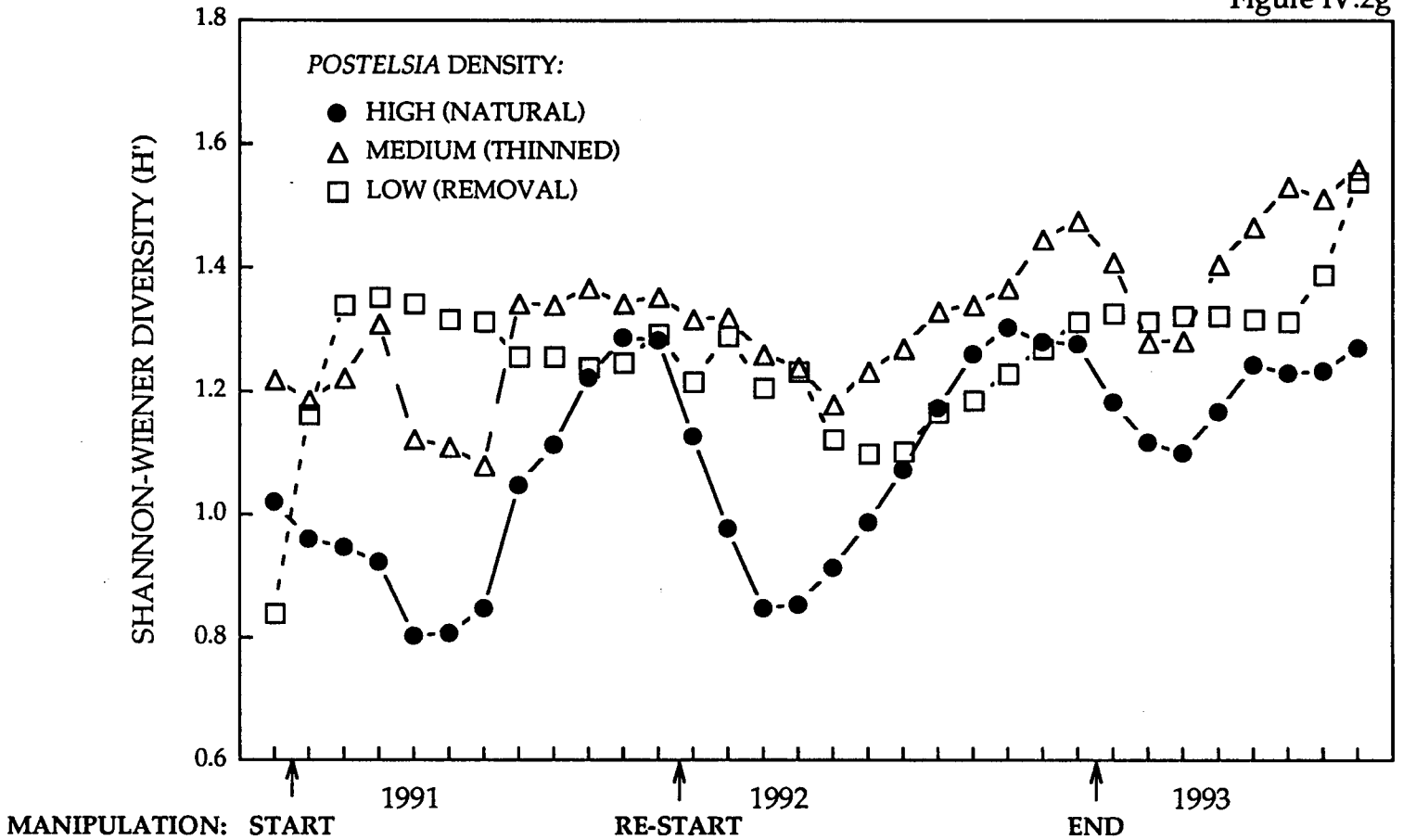
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
REMOVAL	**	*	NS	NS	*	*	NS	NS	NS	NS	*

Figure IV.2f



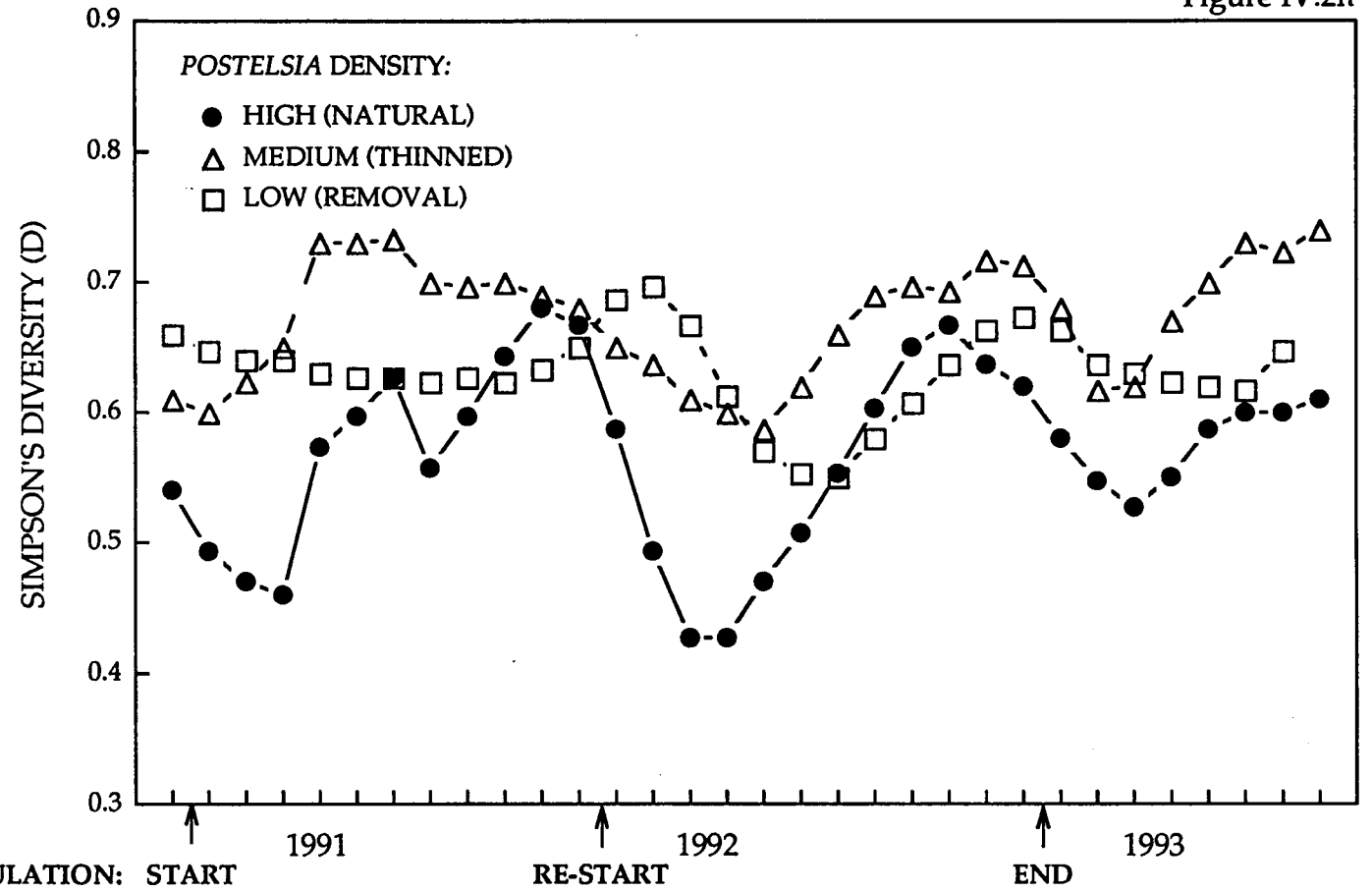
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS
REMOVAL	**	NS	**	**	**	**	**	**	NS	NS	NS

Figure IV.2g



EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	**	*	NS	**	NS	NS	**	*	NS	NS
REMOVAL	**	*	NS	NS	**	NS	NS	NS	*	NS	NS

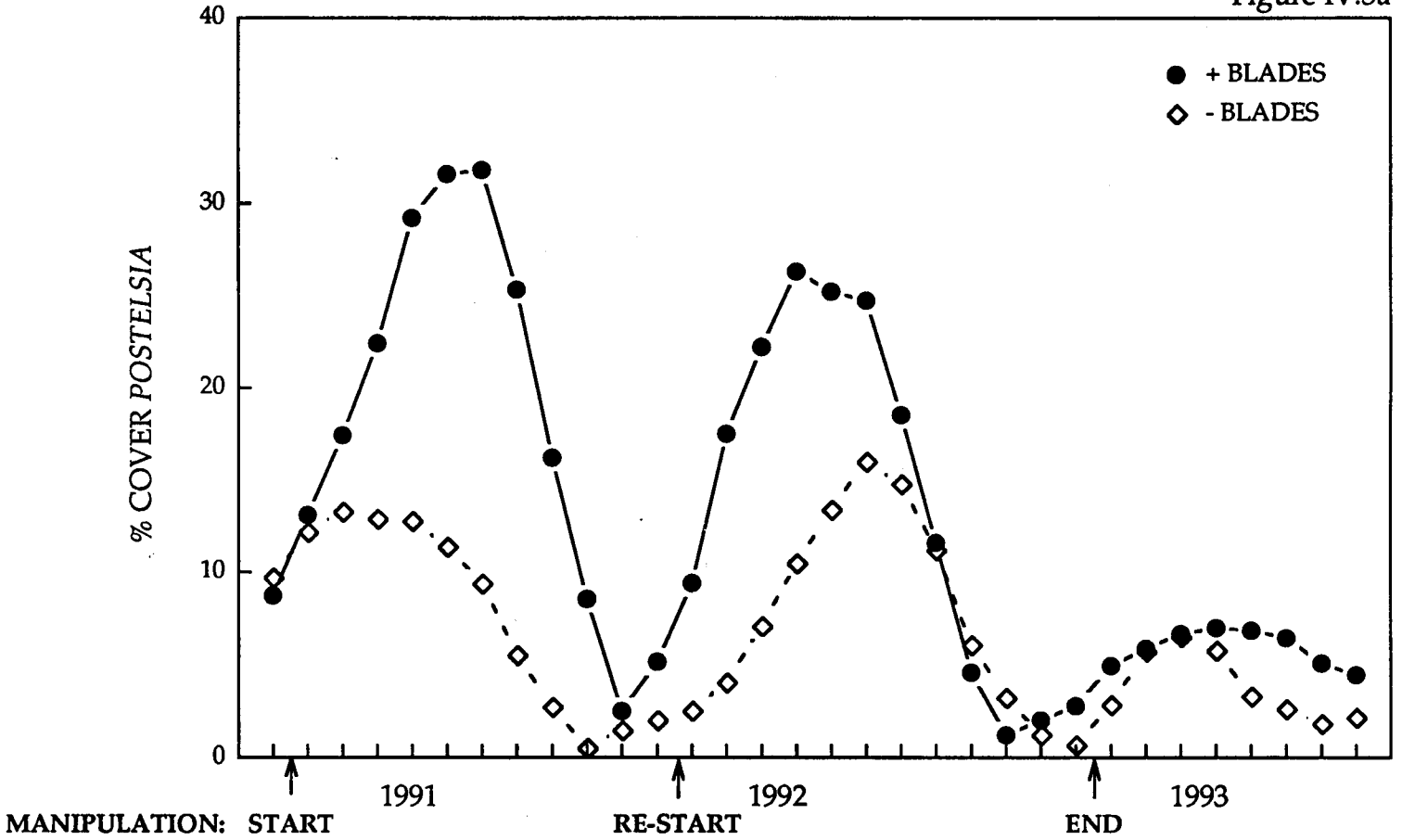
Figure IV.2h



EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
THINNING	NS	**	*	NS	NS	NS	NS	*	*	NS	NS
REMOVAL	*	*	NS	NS	*	NS	**	NS	NS	NS	NS

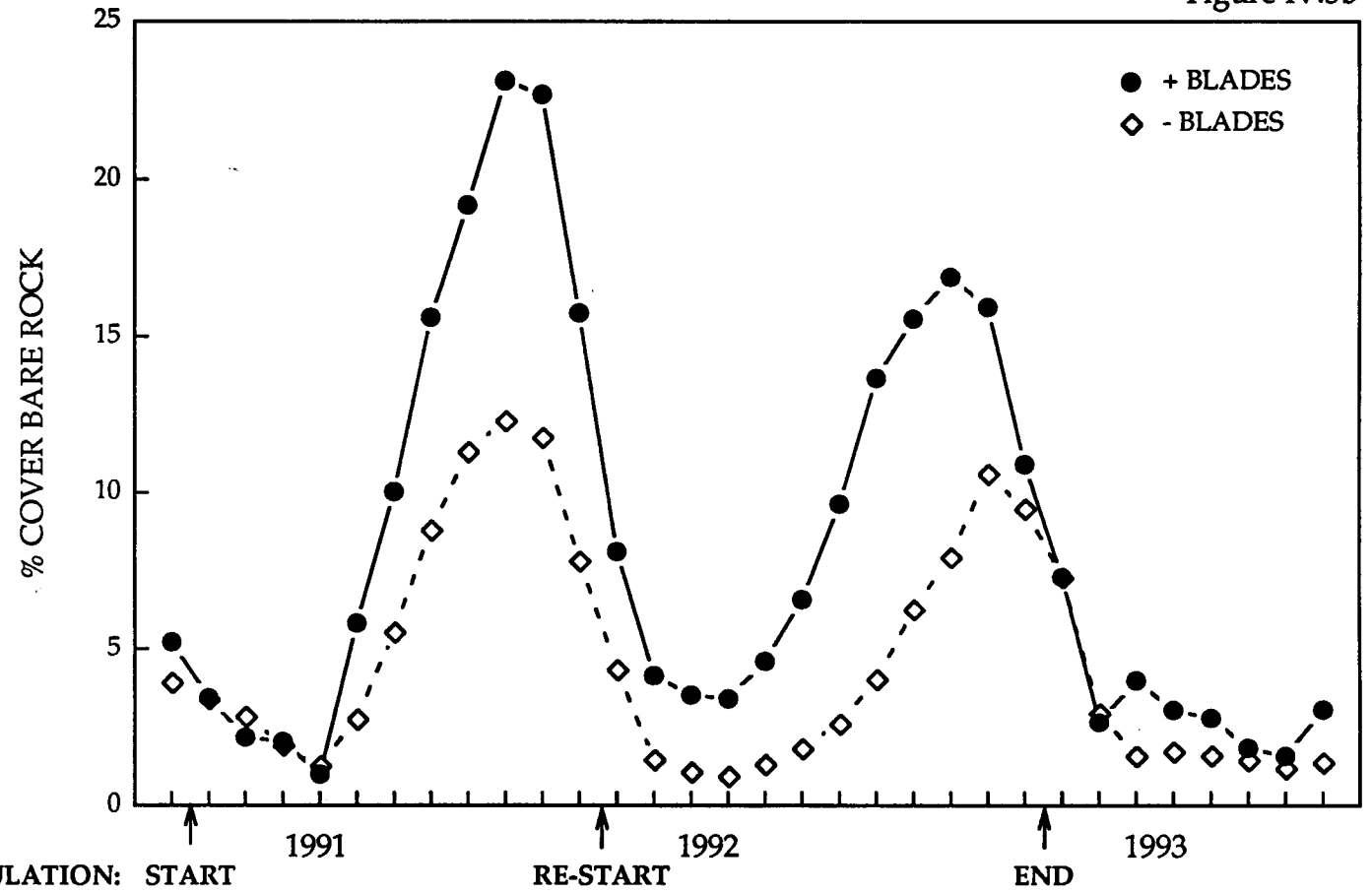
Figure IV.3. Mean primary percent cover of: (a) *Postelsia,* (b) Bare rock, (c) *Odonthalia,* (d) *Corallina,* (e) *Hymenena,* and (f) *Microcladia* and (g) mean Shannon-Wiener species diversity and (h) Simpson's species diversity in unmanipulated plots (solid circles), and blade removal treatments (open diamonds). See caption of Figure IV.5 for further explanation.

Figure IV.3a



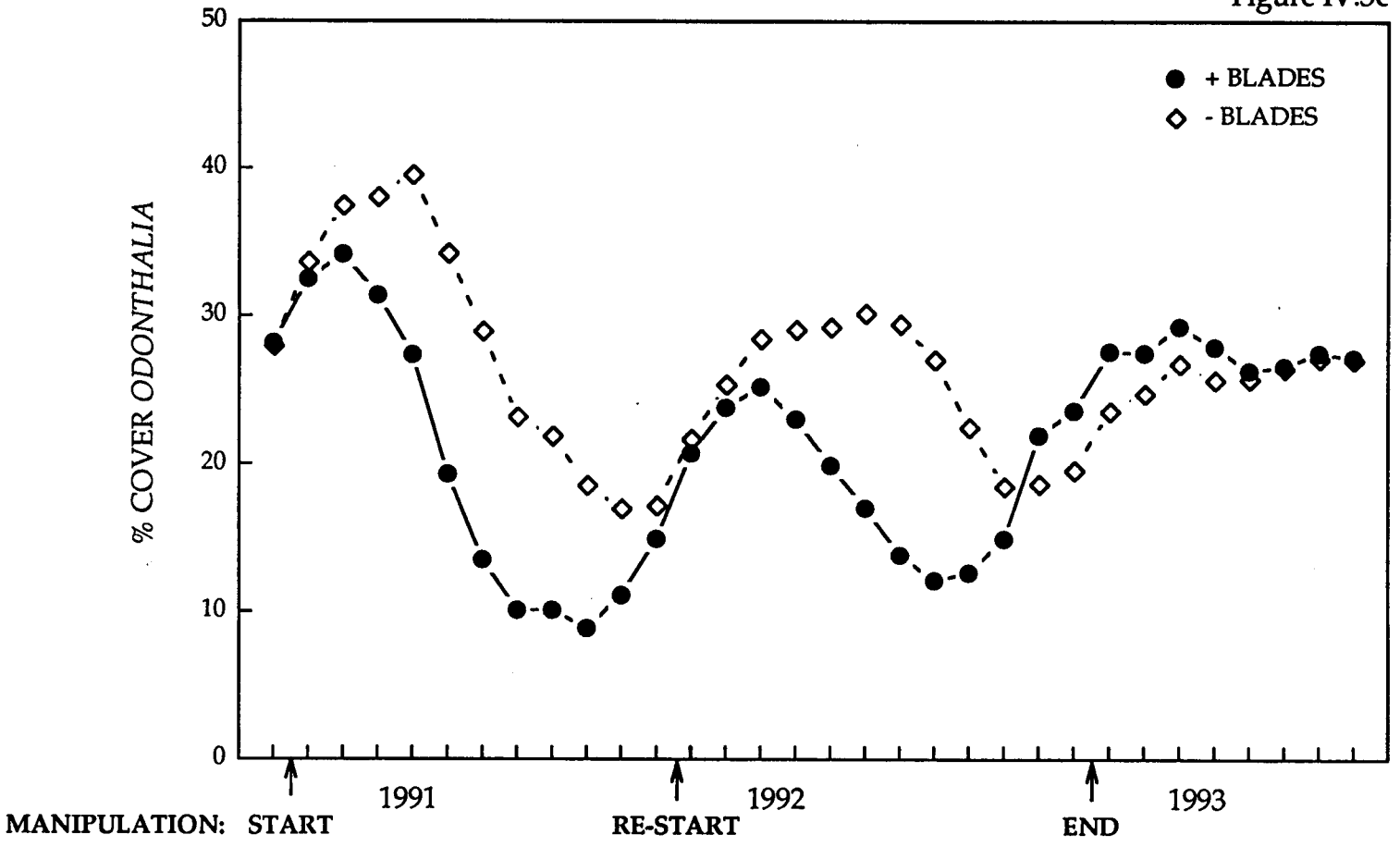
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	**	NS	**	NS	NS	NS	NS	NS	*

Figure IV.3b



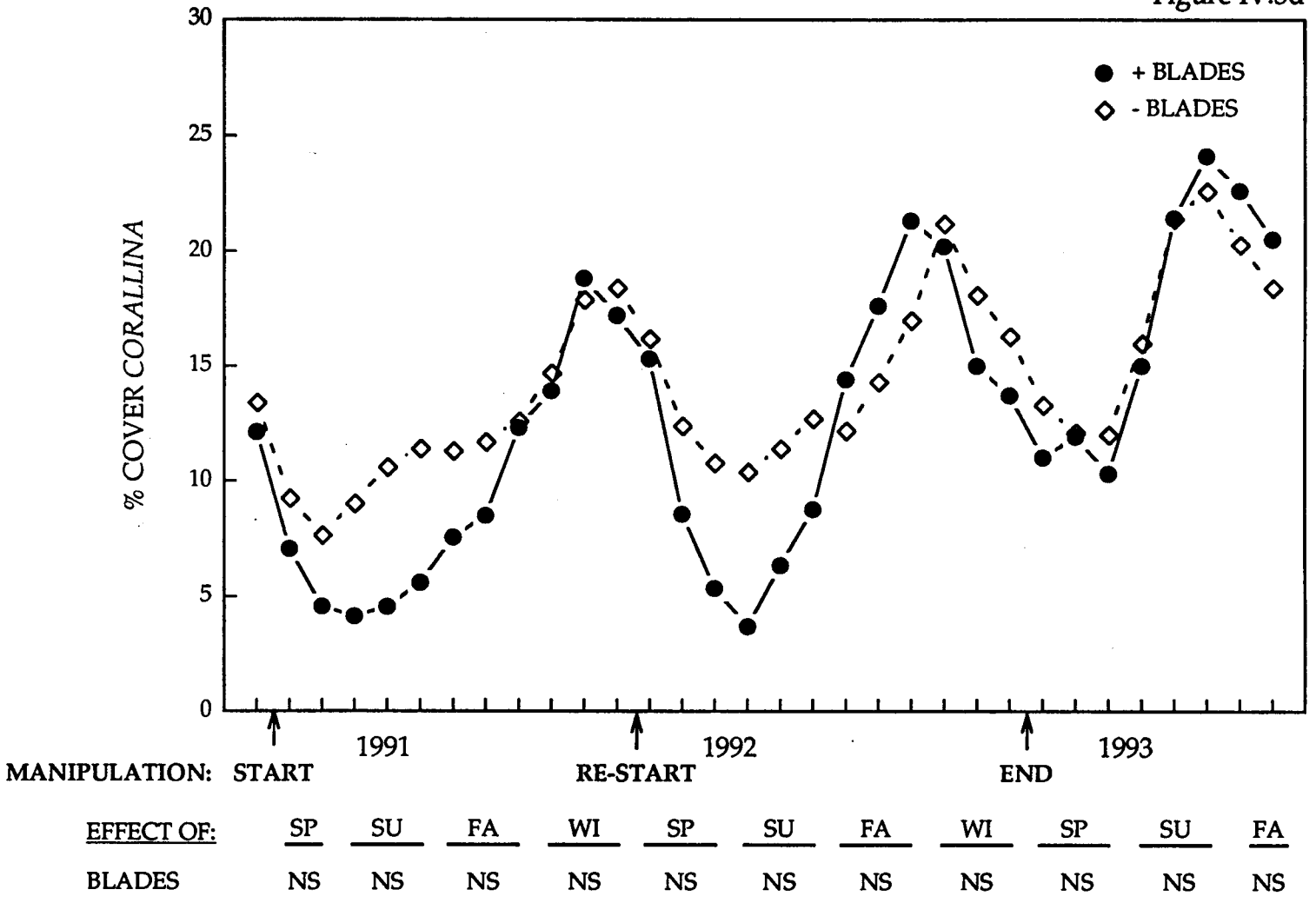
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	NS	NS	NS	NS	*	NS	*	NS	NS

Figure IV.3c



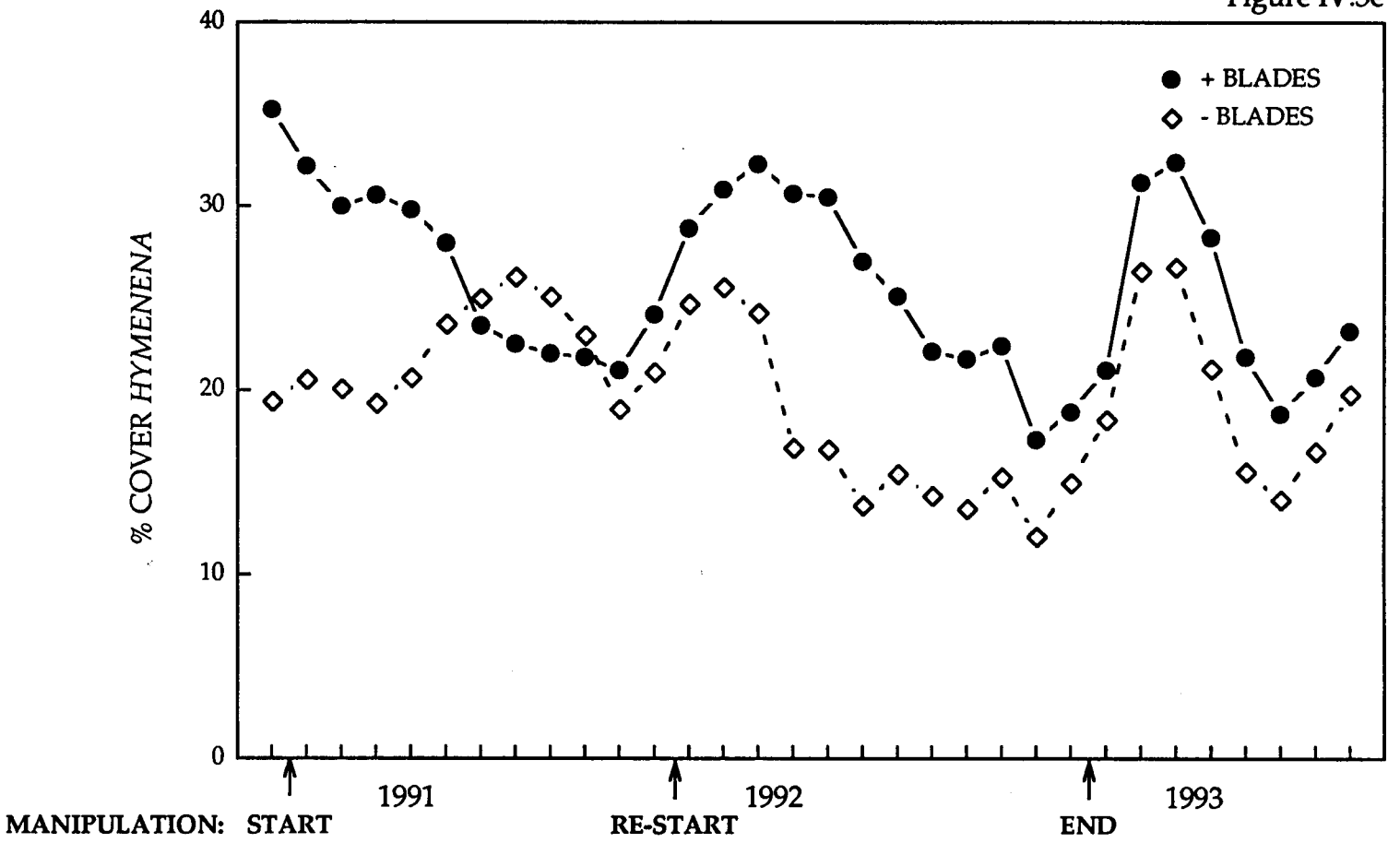
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	**	*	NS	*	NS	NS	NS	NS	NS

Figure IV.3d



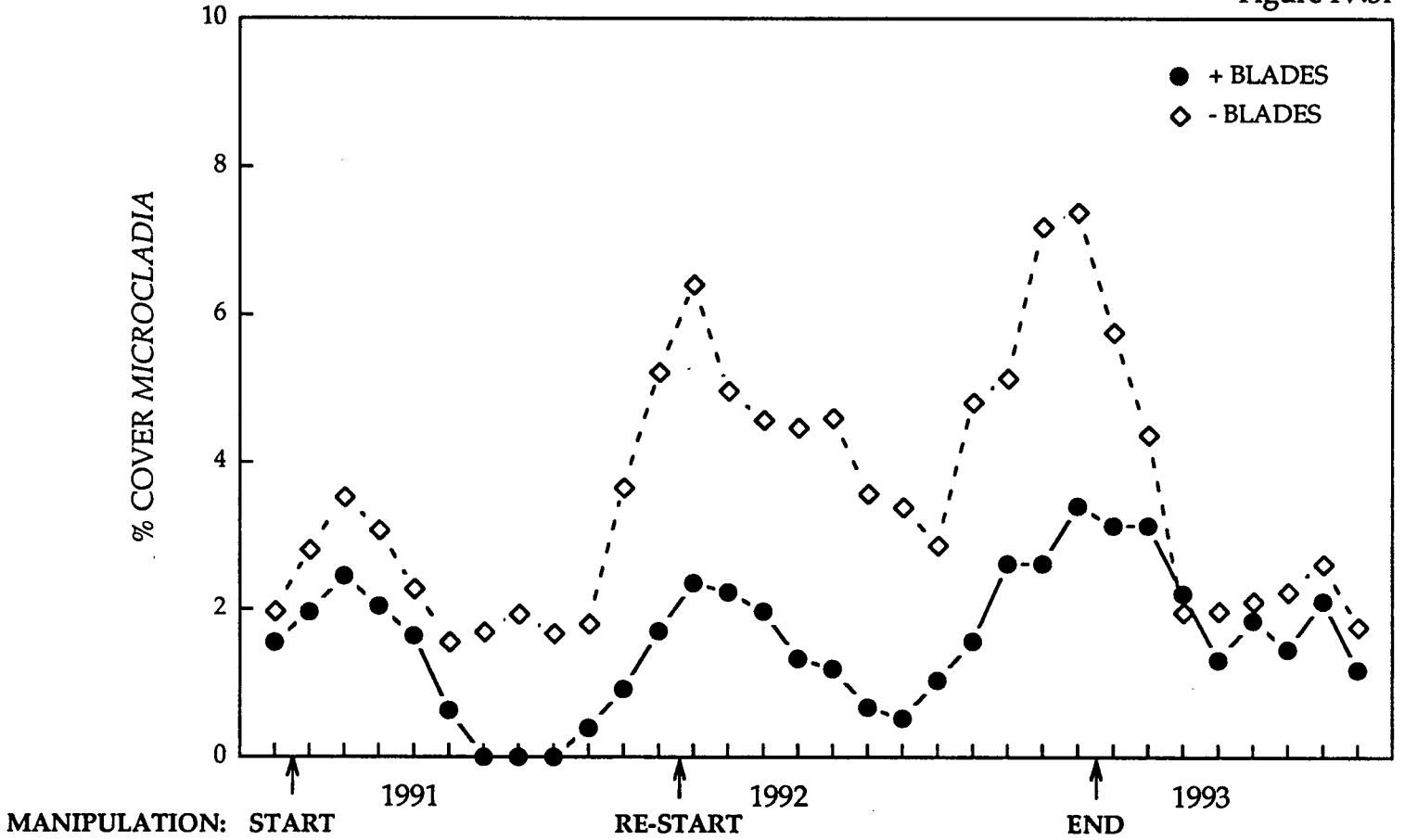
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Figure IV.3e



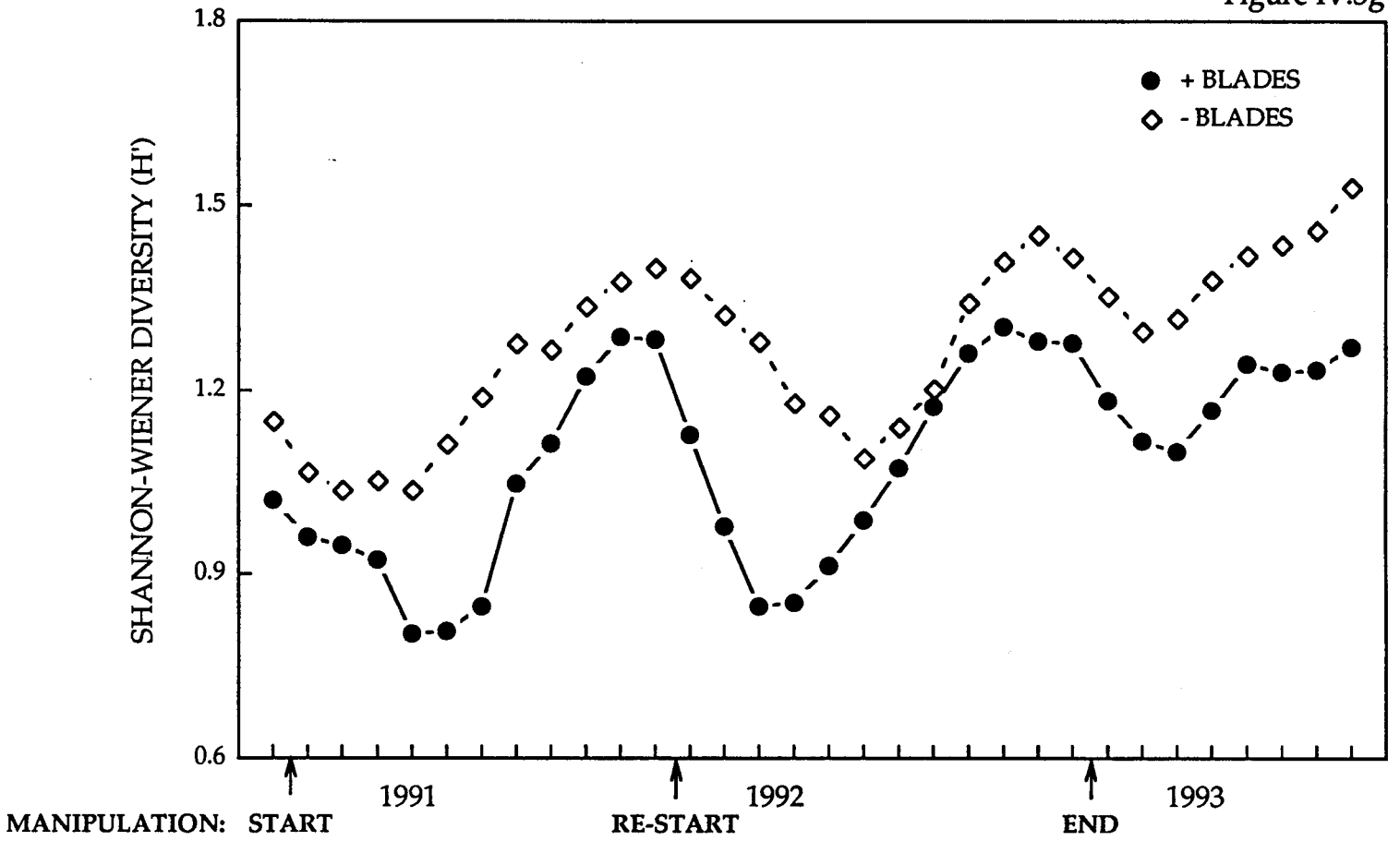
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	*	NS	*	NS	NS	*	NS	NS	NS	*	NS

Figure IV.3f



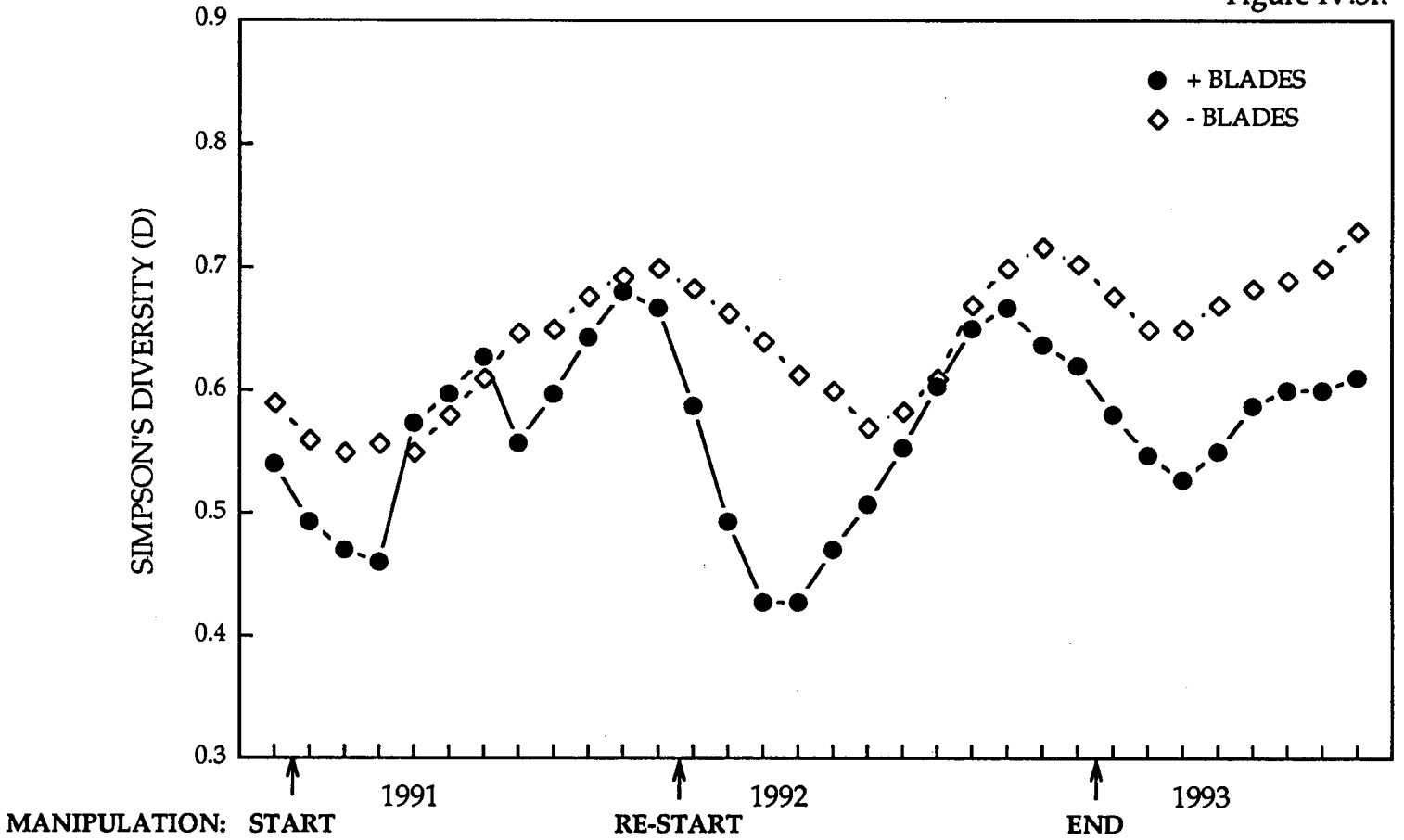
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	**	**	**	**	**	*	NS	NS	NS

Figure IV.3g



EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	NS	NS	*	NS	NS	*	*	NS	NS

Figure IV.3h



EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
BLADES	NS	NS	NS	NS	**	NS	NS	*	*	NS	NS

Figure IV.4. Mean number of limpets (± 1 s.e.m.) in limpet removal plots (stippled bars) and control plots (solid bars) during each season in (a) 1991, (b) 1992 and (c) 1993. Limpets that were counted in the limpet removal plots were removed following the census, so the actual number of limpets present in the plot between the monthly census intervals ranges from zero to the number present at the census. *=$p<0.05$, **=$p<0.01$.

Figure IV.4

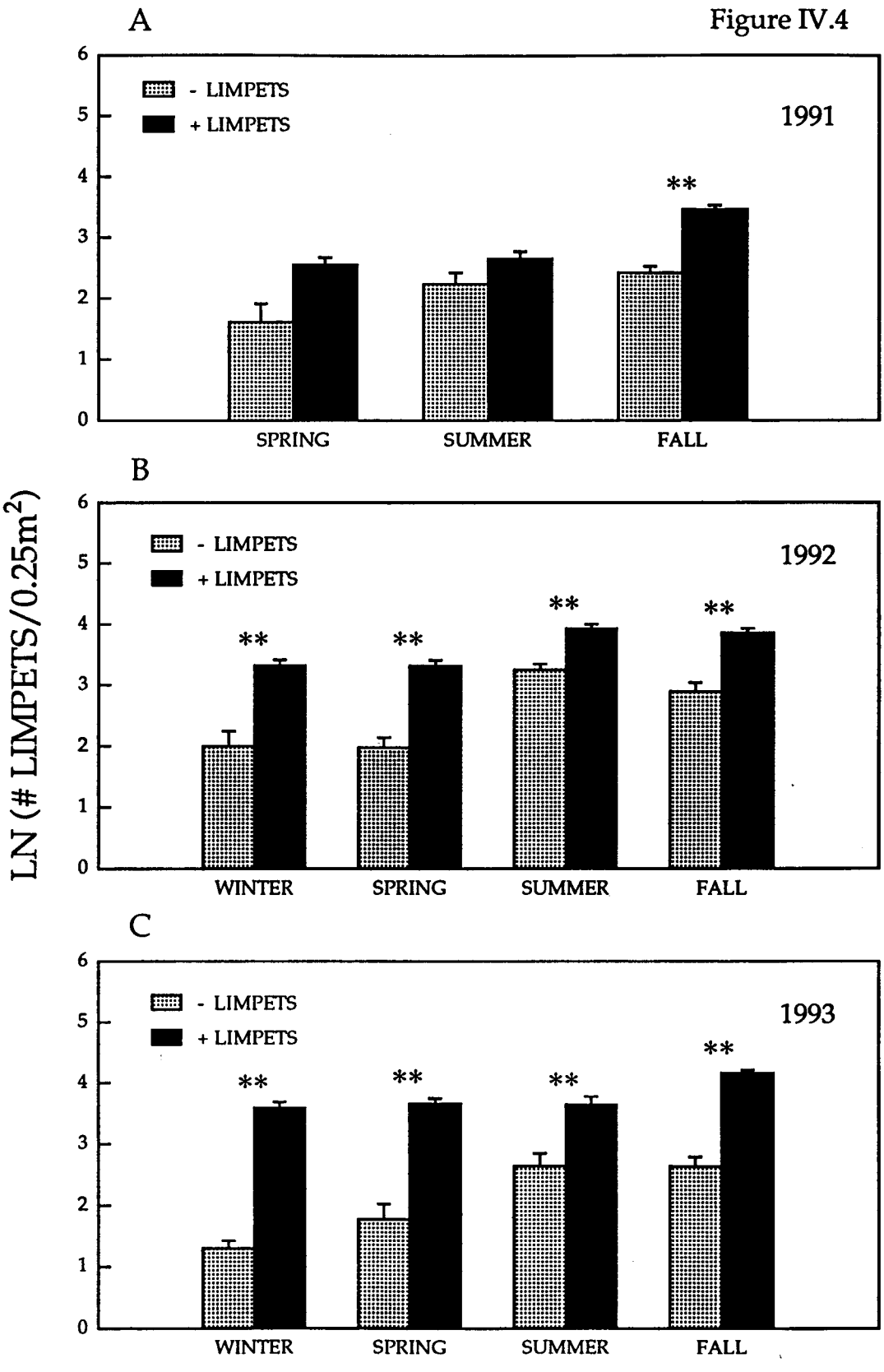

A
- LIMPETS
+ LIMPETS
1991
**
SPRING
SUMMER
FALL
B
LN (# LIMPETS/0.25m²)
1992
WINTER
SPRING
SUMMER
FALL
C
1993

Figure IV.5. Mean number of *Postelsia* (± 1 s.e.m.) in limpet removal plots (stippled bars) and control plots (solid bars) during each season in (a) 1991, (b) 1992 and (c) 1993. *=$p<0.05$, **=$p<0.01$.

Figure IV.5

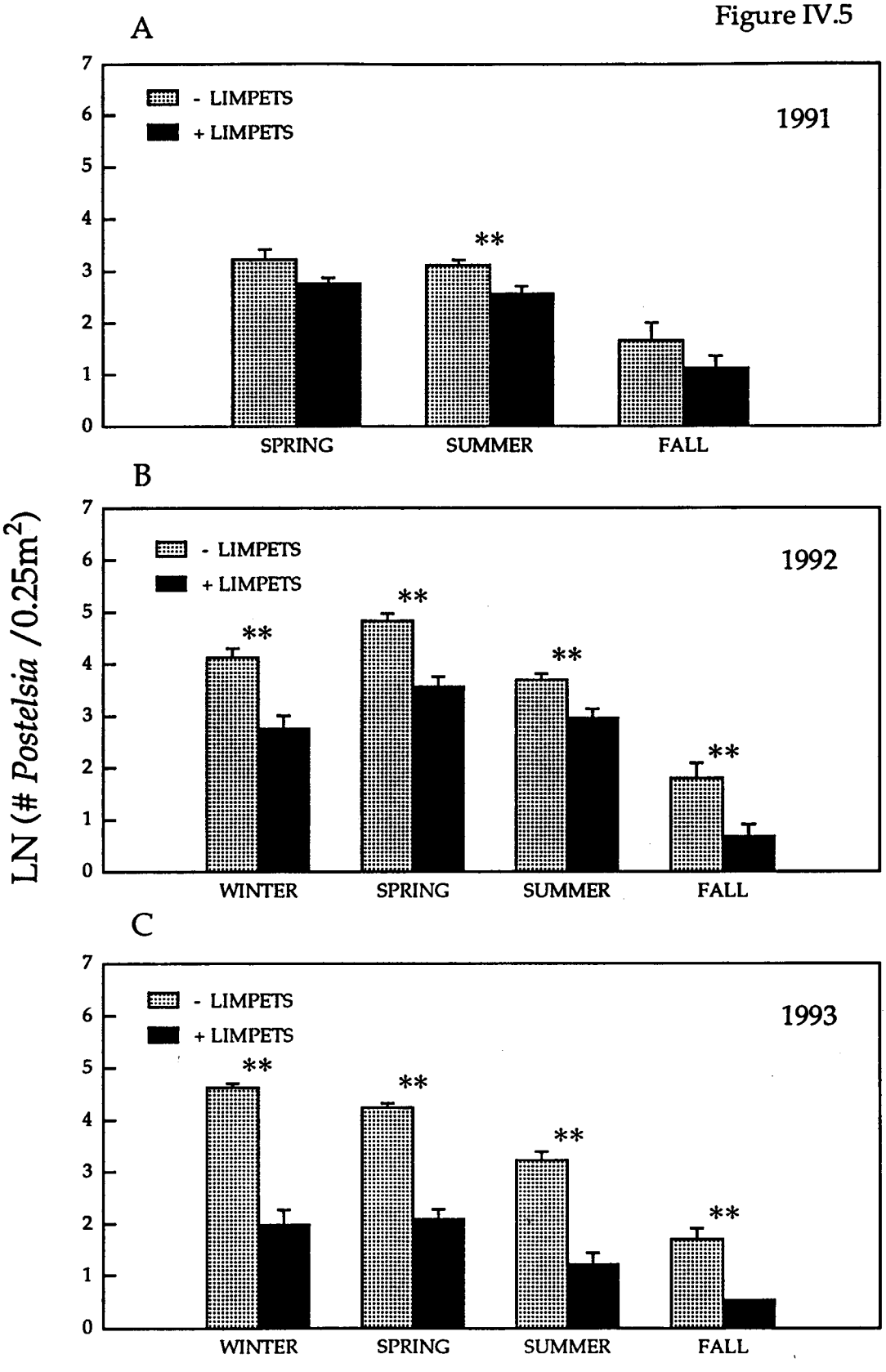

A
- LIMPETS
+ LIMPETS
1991
**
SPRING
SUMMER
FALL
B
LN (# Postelsia /0.25m2)
- LIMPETS
+ LIMPETS
1992
**
**
**
**
WINTER
SPRING
SUMMER
FALL
C
- LIMPETS
+ LIMPETS
1993
**
**
**
**
WINTER
SPRING
SUMMER
FALL

Figure IV.6. Linear regression between the number of limpets and number of *Postelsia* (both log transformed) in the limpet removal and control plots in the spring and summer of (a) 1992 and (b) 1993.

Figure IV.6

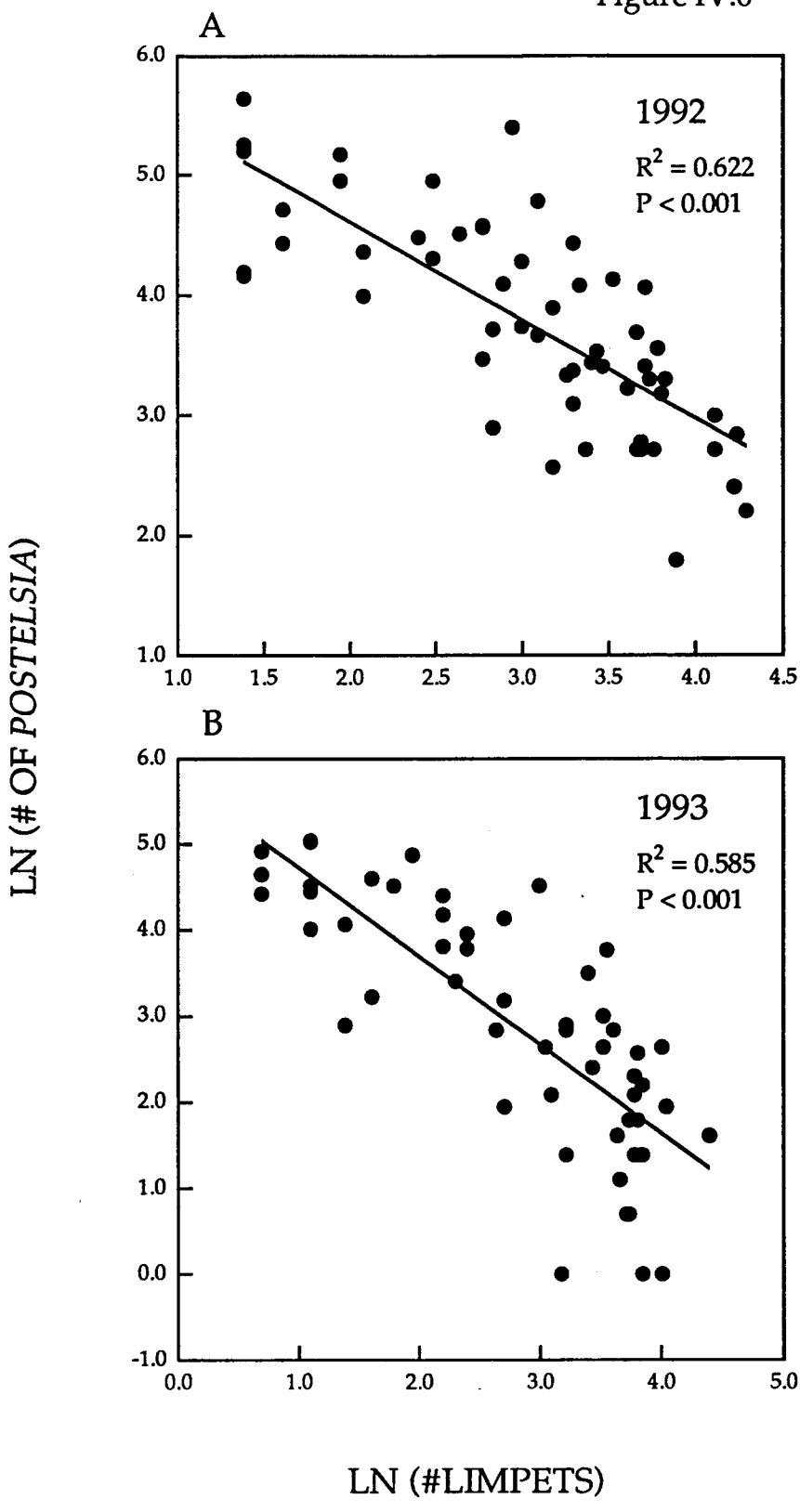

A
1992
$R^2 = 0.622$
$P < 0.001$
B
1993
$R^2 = 0.585$
$P < 0.001$
LN (# OF *POSTELSIA*)
LN (#LIMPETS)

Figure IV.7. Mean stipe lengths (± 1 s.e.m.) of 10 plants randomly chosen from limpet removal plots (sippled bars) and control plots (solid bars) during summer months in (a) 1992 and (b) 1993. *=$p<0.05$, **=$p<0.01$.

Figure IV.7

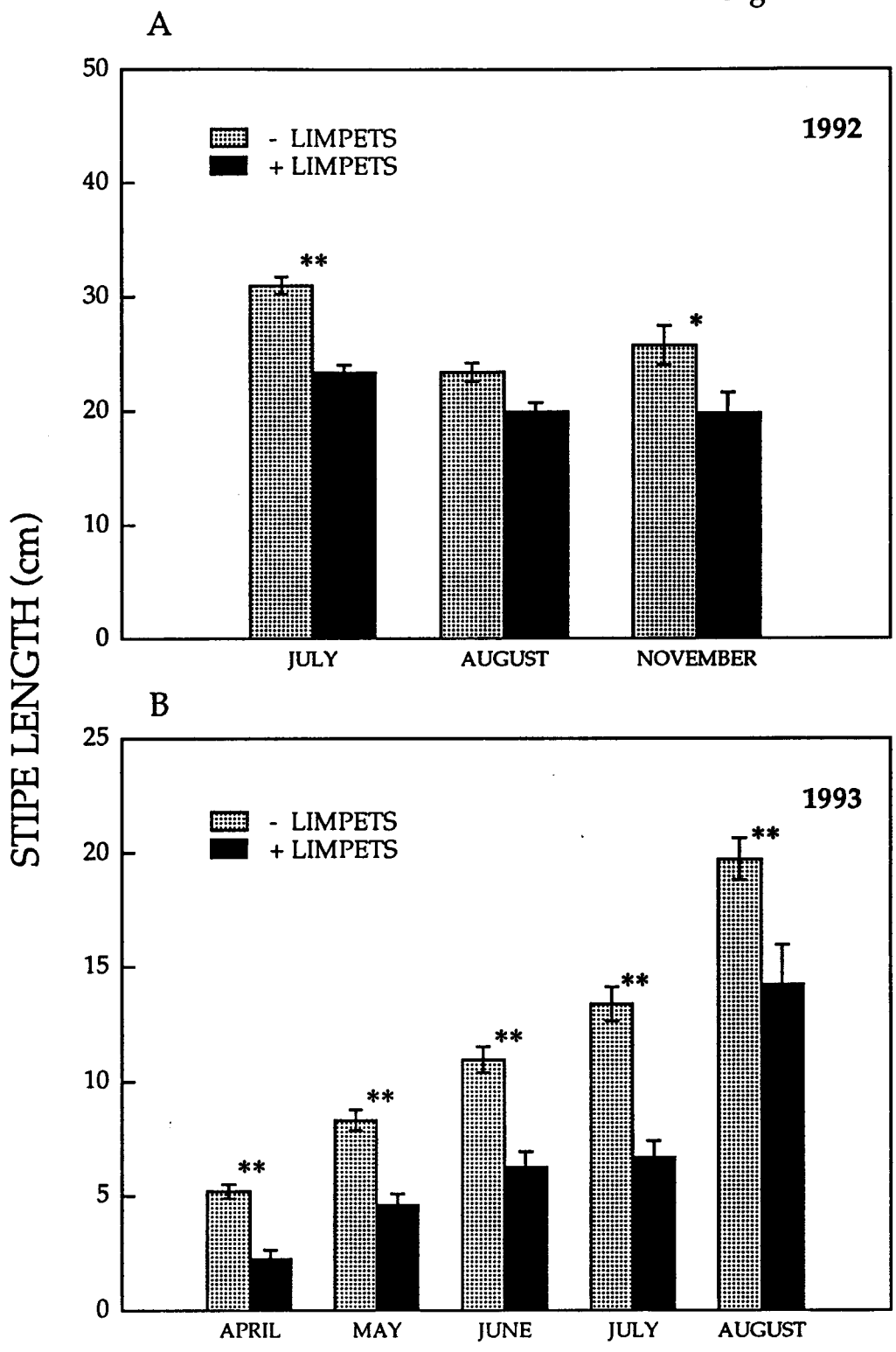
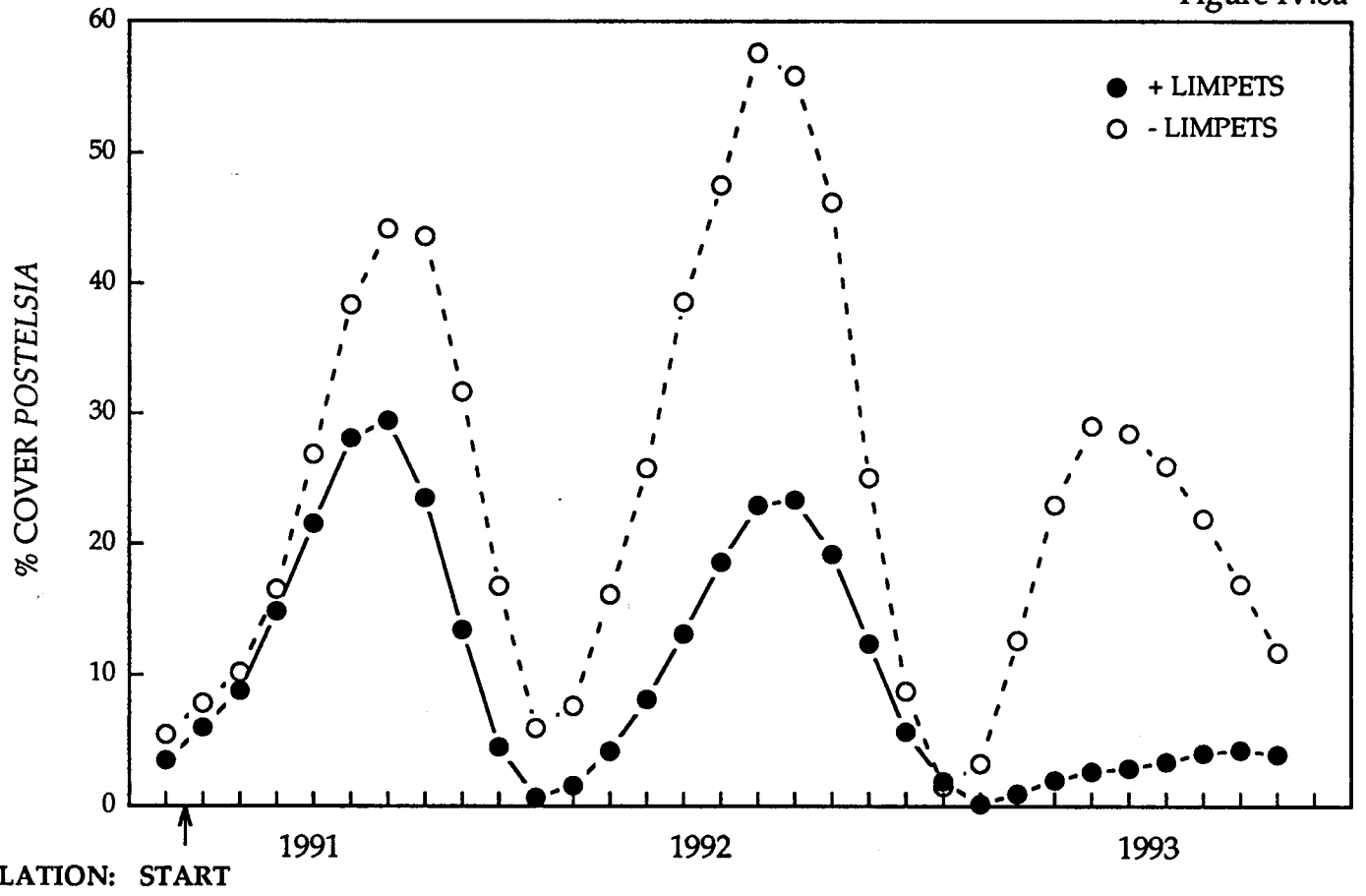

A
1992
- LIMPETS
+ LIMPETS
STIPE LENGTH (cm)
50
40
30
20
10
0
**
*
JULY
AUGUST
NOVEMBER
B
1993
- LIMPETS
+ LIMPETS
25
20
15
10
5
0
**
APRIL
MAY
JUNE
JULY
AUGUST

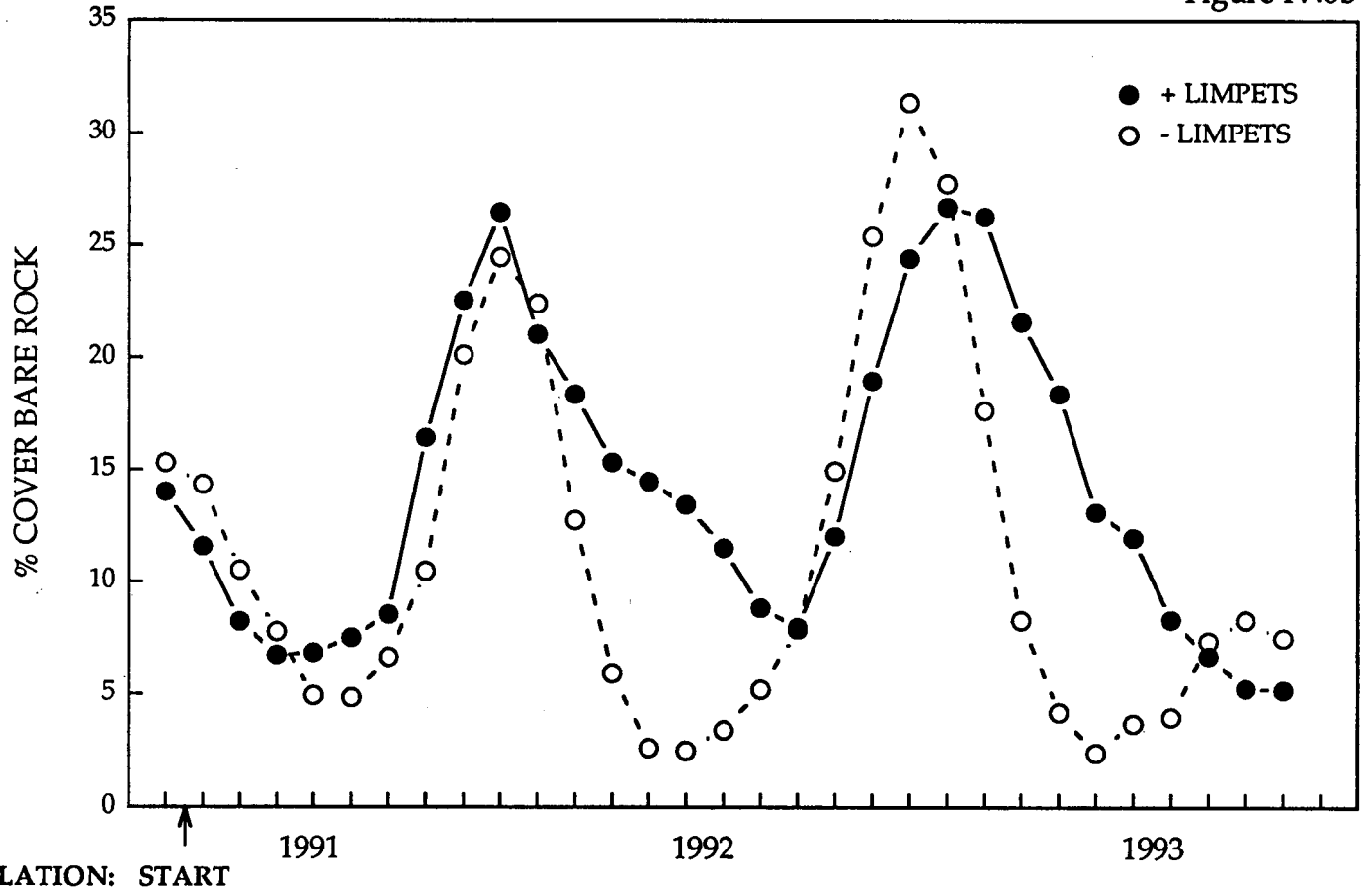
Figure IV.8. Mean primary percent cover of: (a) *Postelsia,* (b) Bare rock, (c) *Odonthalia,* (d) *Corallina,* (e) *Hymenena,* and (f) *Microcladia* and (g) mean Shannon-Wiener species diversity and (h) Simpson's species diversity in unmanipulated plots (solid circles), and limpet removal treatments (open circles). See caption of Figure IV.5 for further explanation.

Figure IV.8a



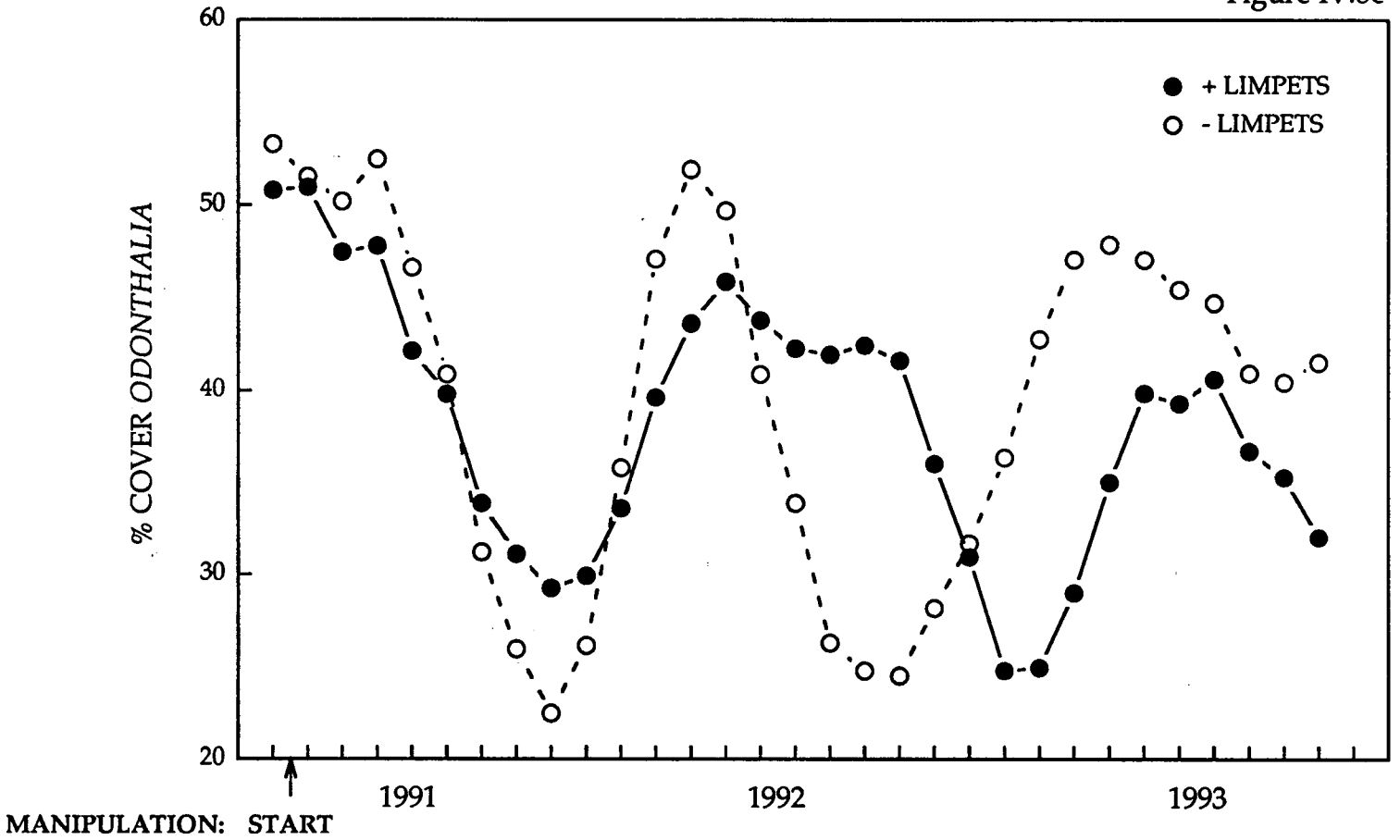
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	**	*	**	**	NS	NS	**	**	*

Figure IV.8b



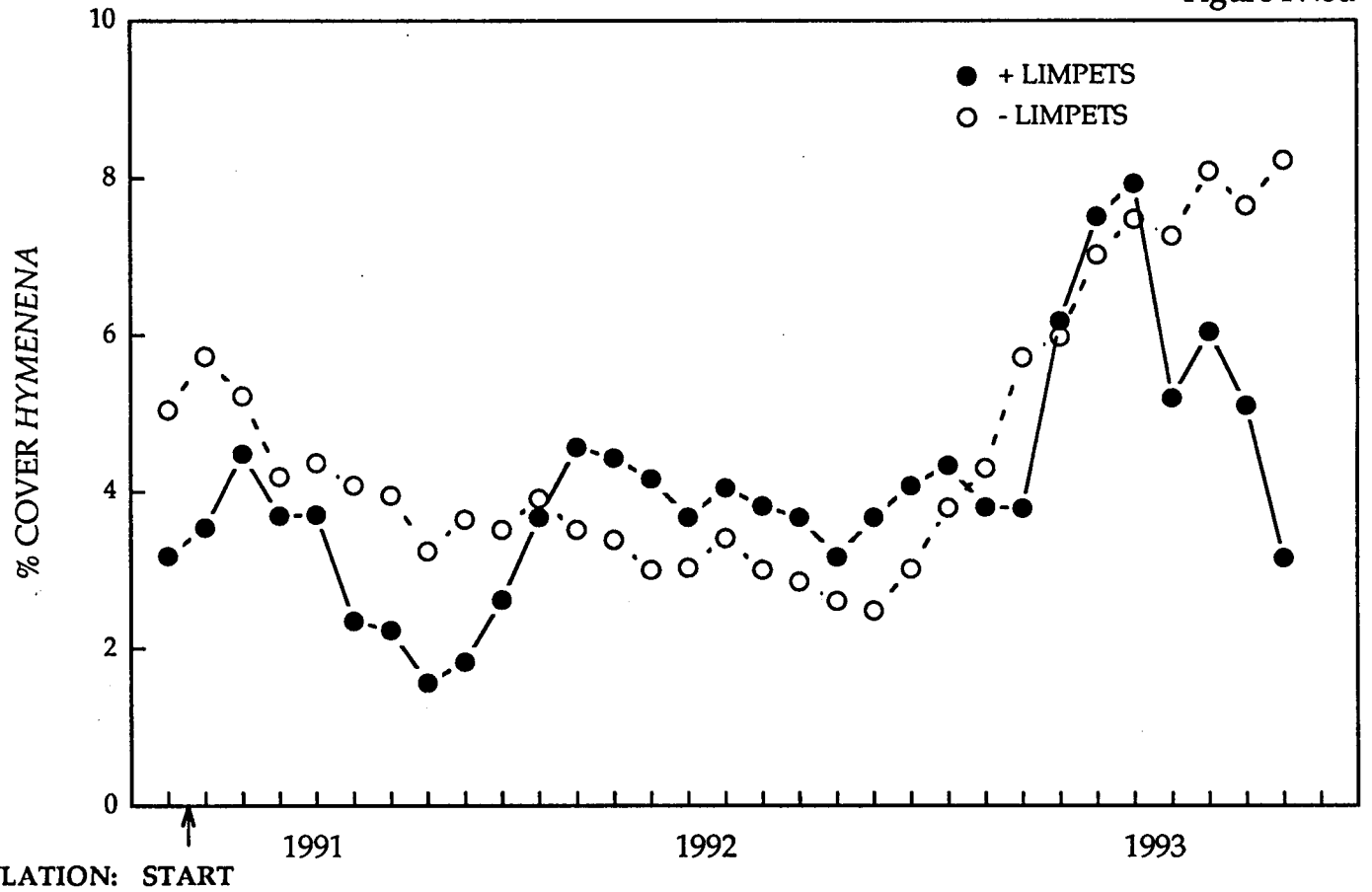
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Figure IV.8c



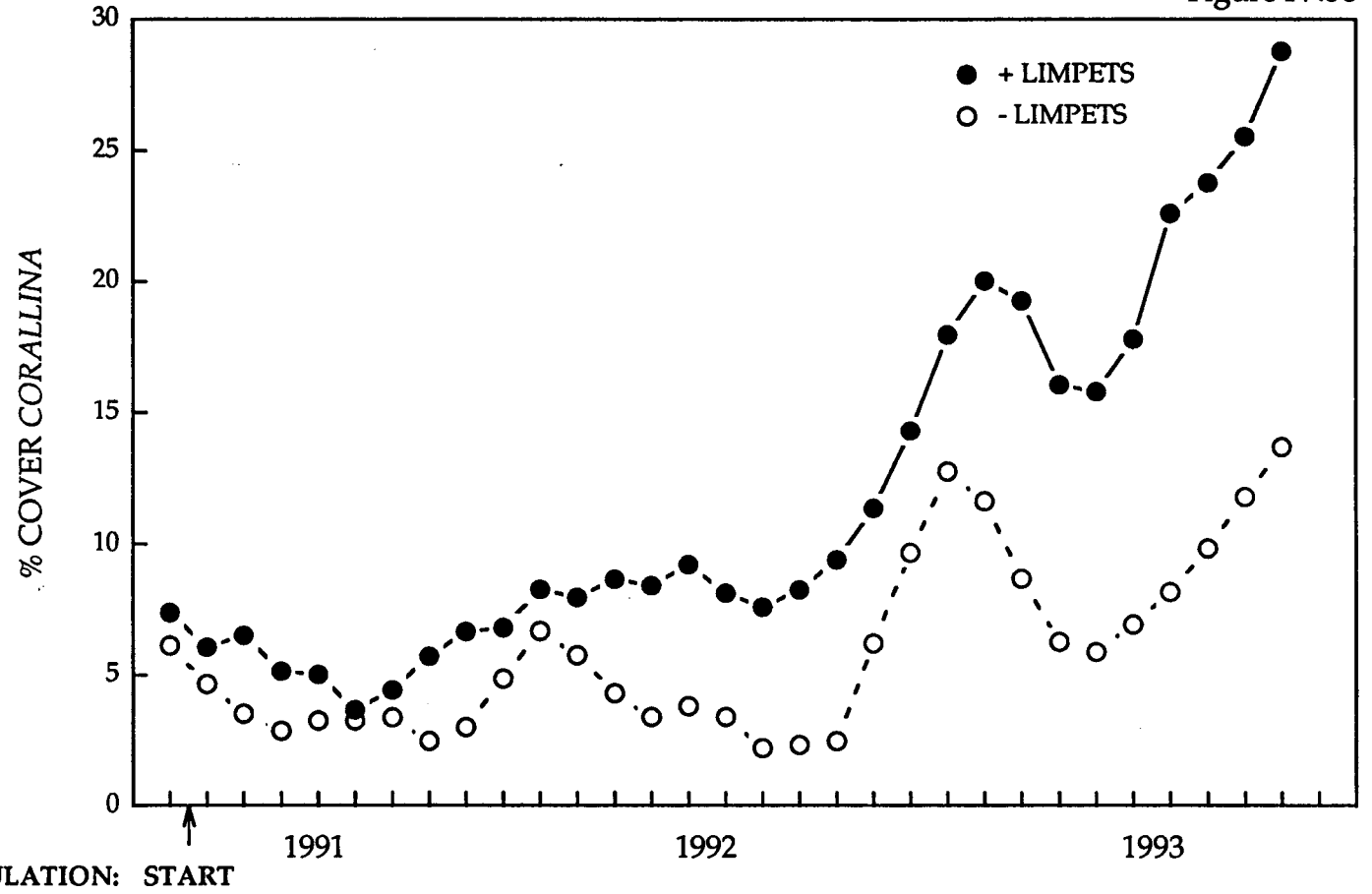
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	NS	NS	NS	**	*	*	NS	NS	NS

Figure IV.8d



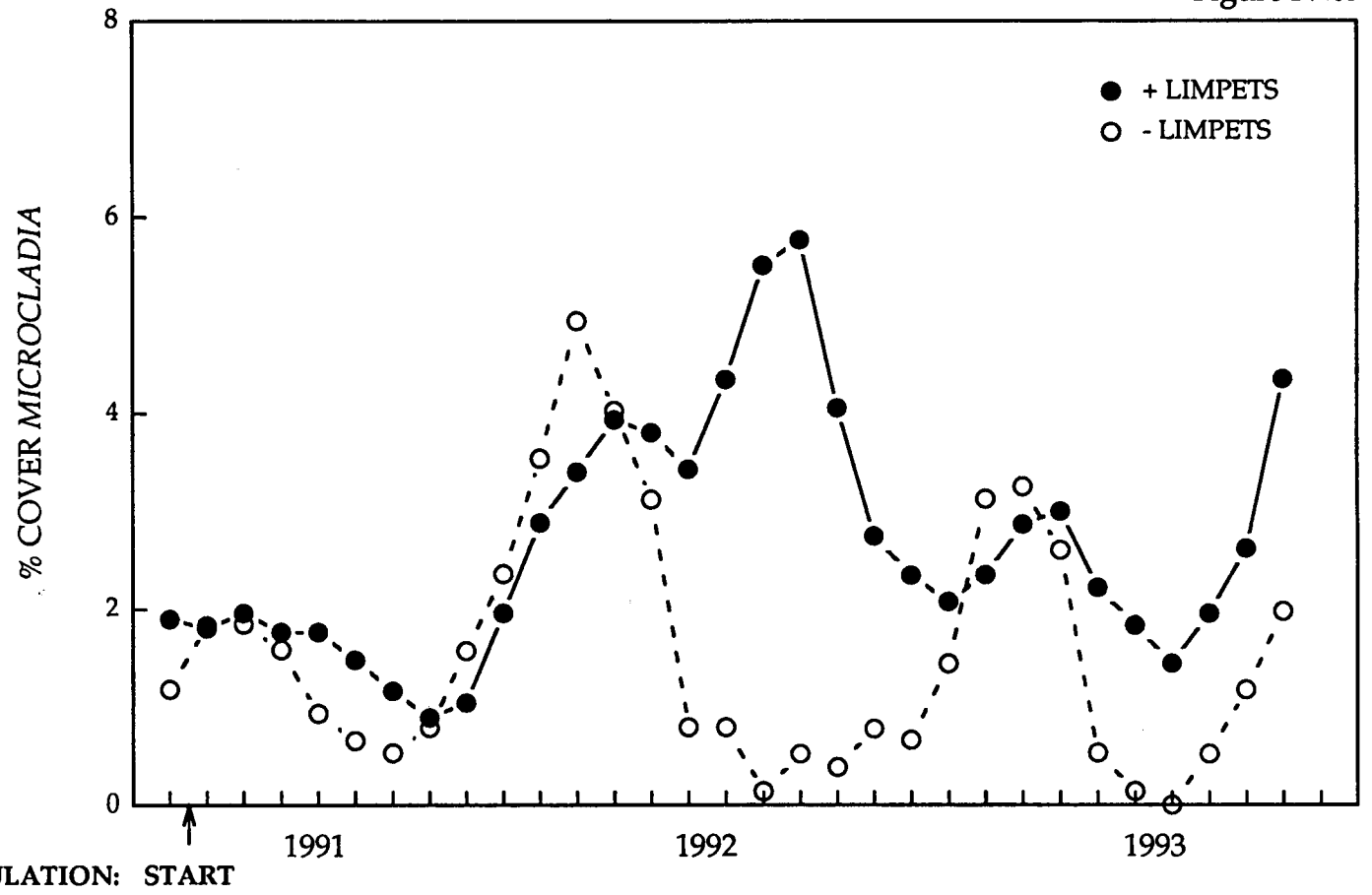
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Figure IV.8e



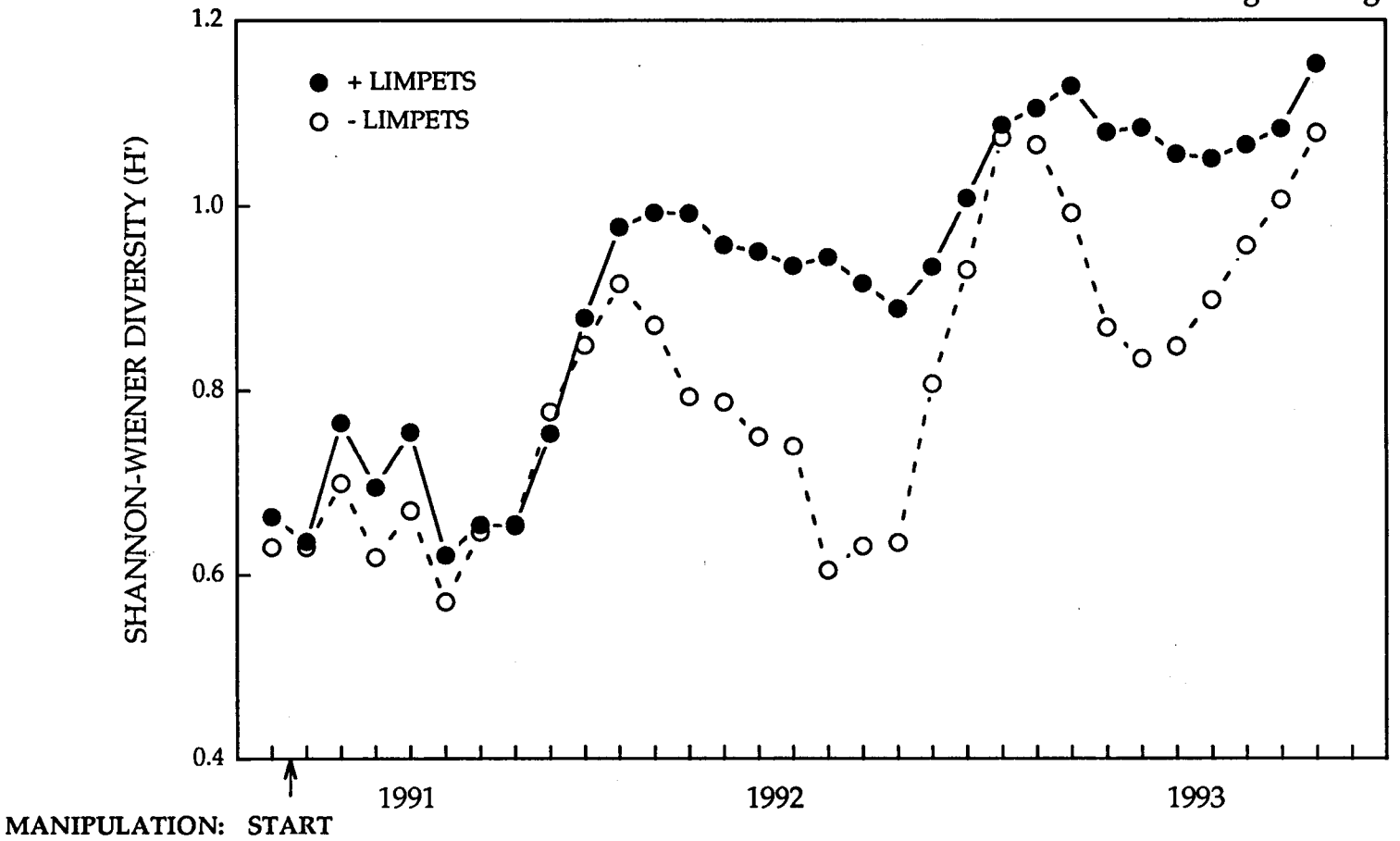
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	*	NS	**	**	**	*	**	**	**

Figure IV.8f



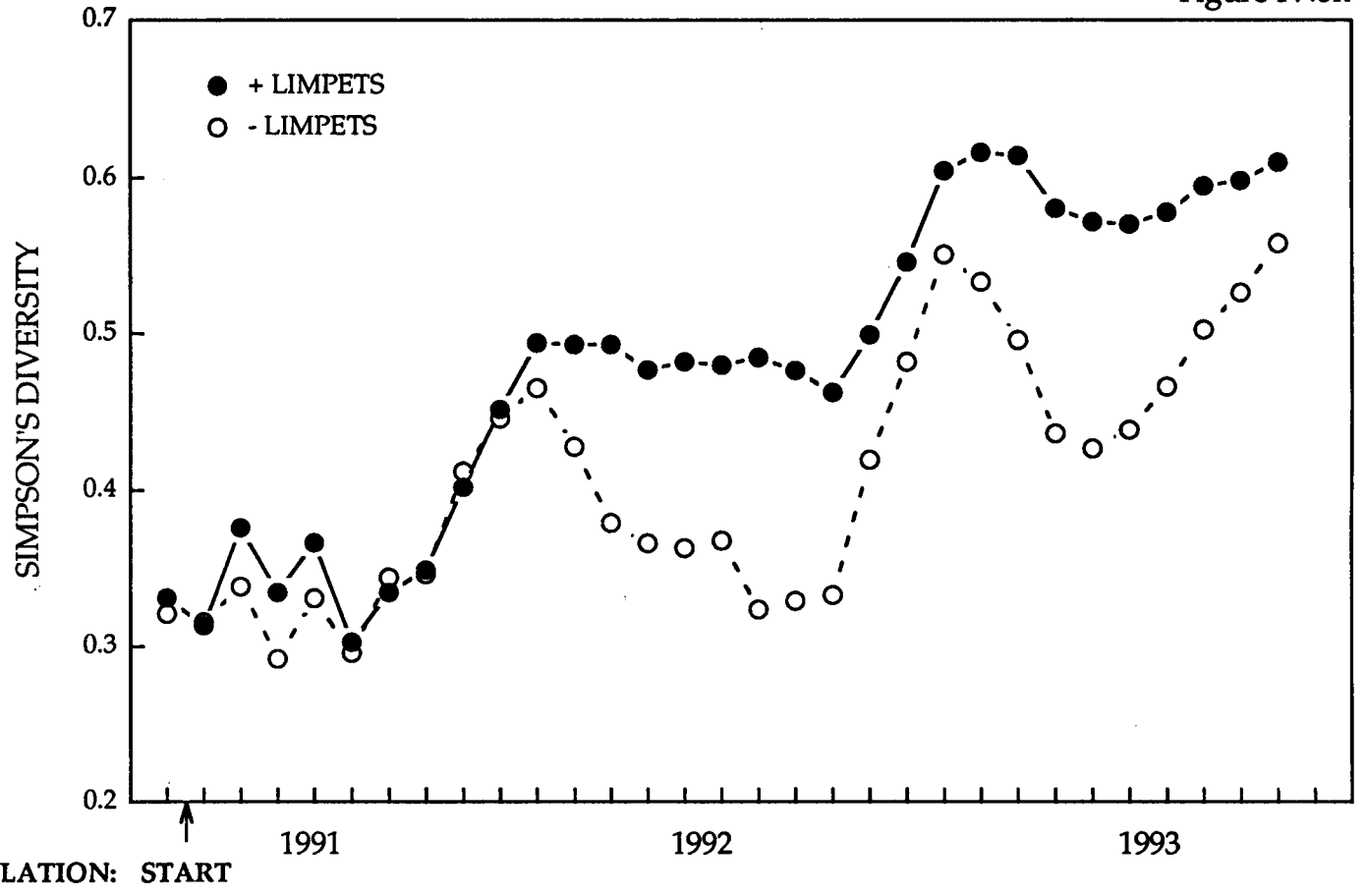
EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	NS	NS	NS	**	**	NS	*	*	NS

Figure IV.8g



EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	NS	NS	*	**	NS	NS	*	*	NS

Figure IV.8h



EFFECT OF:	SP	SU	FA	WI	SP	SU	FA	WI	SP	SU	FA
LIMPETS	NS	NS	NS	NS	**	**	NS	NS	*	*	NS

Chapter V

GENERAL CONCLUSIONS

In this thesis, I have demonstrated how wave-induced disturbances and water motion can affect size, growth, survival, recruitment and ultimately influence community structure of marine, intertidal macrophytes. Intertidal seaweeds seem extremely well adapted for life in the physically harsh environment of the wave-swept intertidal, where plants must deal with the stresses of emersion and desiccation at low tide, and are susceptible to dislodgment by waves during stormy, high tide periods. As stated by Norton (1991), "Seaweeds not only survive in the intertidal zone, they often dominate it."

Intertidal plants such as *Fucus gardneri* are extremely successful in the intertidal due to their ability to modify their size and shape to suit the prevailing conditions. Hydrodynamic forces from waves have a large influence on the sizes to which *Fucus* plants can grow, and the results of the models of predicted optimal sizes fall very close to the mean sizes of plants observed in the field. Plants seem to be able to grow as large as the environment will allow while maintaining a relatively high probability of survival. The transplant experiment provided empirical support for the idea that wave forces can set mechanical limits to size in *Fucus* and that wave exposure has a direct influence on plant size, but not on survival.

Seaweeds, such as *Postelsia* take advantage of the seasonal variation in wave disturbance by having heteromorphic life histories. *Postelsia* 's annual life history of seems ideally suited to life in a seasonally disturbed

environment. Areas of mussel beds that were disturbed by wave action in the winter had the highest recruitment of *Postelsia* in the following spring, presumably because the sea palm propagules were able to survive beneath the mussel bed in fall and were somehow stimulated to germinate by the occurrence of a winter disturbance. Although the dispersal of sea palm spores was limited in distance, there may have been some secondary short distance dispersal at the gamete stage or via mobile animals. *Postelsia* seem to be restricted to wave exposed areas due to optimal physical conditions at these sites that enhance growth, and are not able to survive and grow in wave protected areas, even in the absence of competition for space. Zonation of sea palms with respect to tidal height seems to be controlled by the preference of *Postelsia* for physiological conditions provided by intermittent exposure to air and constant stirring of blades and splashing present at mid zone wave exposed sites.

Postelsia is also extremely successful in wave-exposed environments due to its ability to reproduce prolifically and grow rapidly. The haptera of *Postelsia* can grow out over the understory algal turf as long as the holdfast is in contact with the bare rock at some point. *Postelsia* are ripped from the rock in winter, and bare rock space is renewed when the *Postelsia* holdfasts dislodge sections of overgrown turf. Predation, competition and disturbance all play important roles in structuring this community. Grazing limpets play a major role in maintaining high levels of diversity in the algal understory community. Limpets indirectly contribute to the high species diversity in the understory by grazing *Postelsia*, thereby decreasing its abundance and competitive advantage over other understory species. Competition for space in the understory is very intense and bare

rock space is quickly occupied. Disturbances which dislodge *Postelsia* and many overgrown understory species from the rock each winter play an important role in maintaining a high level of diversity in the algal understory and in providing a suitable "foothold" for *Postelsia* to spread from year to year. These annual disturbances prevent the monopolization of space by fast growing turfy species like *Corallina,* and may provide other less competitive, and perhaps relatively rare species a chance to settle and grow.

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